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Factors influencing the distribution of brown trout (Salmo trutta) in a mountain stream: Implications for brown trout invasion success

Christy Meredith
Utah State University

FACTORS INFLUENCING THE DISTRIBUTION OF BROWN TROUT (*SALMO TRUTTA*) IN A MOUNTAIN STREAM: IMPLICATIONS FOR BROWN TROUT INVASION SUCCESS

by

Christy Meredith

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Approved:

Phaedra Budy Major Professor	Brett Roper Committee Member
Mevin Hooten Committee Member	John C. Schmidt Committee Member
Chris Luecke Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

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Logan, Utah

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ABSTRACT

Factors influencing the distribution of brown trout (*Salmo trutta*) in a mountain stream: Implications for brown trout invasion success

by

Christy Meredith, Doctor of Philosophy

Utah State University, 2012

Major Professor: Dr. Phaedra Budy
Department: Watershed Sciences

Brown trout (*Salmo trutta*), one of the world's most successful introduced species, negatively impacts native aquatic communities through predation, competition, and ecosystem-level effects. Thus, there is a need to understand factors controlling the distribution of exotic brown trout in river systems, in order to prioritize and develop conservation and management strategies. Within the context of invasion success, I investigated how the physical template of the Logan River influences the distribution of brown trout along a longitudinal gradient, and the potential for brown trout predation on the native mottled sculpin (*Cottus bairdi*). The Logan River, Utah USA, is a high-elevation, mountain river exhibiting a wide range of physical habitat characteristics along the altitudinal (or elevational) gradient.

In chapter 1, I evaluated whether longitudinal trends in geomorphology contribute to higher potential mortality of brown trout fry at high elevations due to flood-caused streambed scour. High-elevation spawning gravels did not exhibit higher scour compared to low elevations, because brown trout locally chose low-scour areas for spawning. In chapter 2, I investigated the importance of gravel availability, versus other habitat factors, in controlling the spatial distribution of brown trout redd densities. Using a Bayesian hierarchical modeling approach, I

demonstrated that anchor ice, distance from high-quality backwater habitat, and to a lesser-extent gravel availability, best explained redd densities. Finally, in chapter 3, I evaluated the potential predatory effects of exotic brown trout on native mottled sculpin (*Cottus bairdi*). High rates of sculpin consumption contrasted to previously documented low rates of predation by native Bonneville cutthroat (*Oncorhynchus clarkii*) and depended on abiotic factors controlling the distribution of both species.

Collectively, my research suggests that both abiotic factors and source-population dynamics structure brown trout distributions on the Logan River, and ultimately the potential impacts of this invasive fish. Specifically, the distribution of anchor ice and distance from dam backwaters are important drivers of the brown trout distribution, which may extend to other systems. These drivers, including how they may be influenced by future climate change and habitat alteration, should be considered in management efforts to control brown trout expansion and to limit the predatory impacts of brown trout.

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PUBLIC ABSTRACT

Factors influencing the distribution of brown trout (*Salmo trutta*) in a mountain stream: Implications for brown trout invasion success

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Brown trout (*Salmo trutta*), one of the world's most successful introduced species in river and lake systems, negatively impacts native species through predation, competition, and system-wide effects. Thus, there is a need to understand factors controlling the distribution of brown trout, in order to prioritize and develop conservation and management strategies. Within the context of invasion success, I investigated how the physical characteristics of the Logan River influence the distribution of brown trout, as well as the potential for brown trout predation on a native fish, the mottled sculpin (*Cottus bairdi*).

In chapter 1, I evaluated whether changes in the river from downstream to upstream contribute to potentially higher mortality of larval brown trout during flood events, due to the movement of substrates where these early life-stages develop. Potential mortality was not greater at high elevations, because brown trout locally chose low-movement areas to deposit their eggs. In chapter 2, I investigated the importance of spawning gravel availability, versus other habitat factors, in influencing the density of eggs deposited by brown trout. Winter ice conditions, distance from a reservoir, and to a lesser-extent the availability of small substrates, best explained the density of brown trout egg locations. Finally, in chapter 3, I evaluated the potential predatory effects of exotic brown trout on native mottled sculpin (*Cottus bairdi*). The diets of brown trout

consisted of a high percentage of sculpin, which contrasted to a low percentage in diets previously documented for native Bonneville cutthroat (*Oncorhynchus clarkii*) on the Logan River.

My research suggests that winter ice conditions and distance from reservoirs are important drivers of the brown trout distribution, which could extend to other systems. These drivers, including how they may be influenced by future climate change and habitat alteration, should be considered in management efforts to control brown trout expansion and to limit the predatory impacts of brown trout.

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Christy Starr Meredith

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CHAPTER 1

INTRODUCTION

The introduction of invasive species is considered to be one of the leading causes of native species decline worldwide (Wilcove et al., 1998; Mooney and Cleland, 2001). Invasive species have impacts on native communities through mechanisms such as competitive exclusion, niche displacement, and predation (Mooney and Cleland, 2001). In response to potentially large negative impacts to native communities, many scientific efforts have focused on determining the factors that most contribute to invasion success (Williamson and Fitter, 1996; Lake and Leishman, 2004; Marchetti et al., 2004). Ultimately, this knowledge can be used to minimize the spread of the worst invaders into high-quality ecosystems.

Similar factors contribute to invasion success across many different ecological systems, including propagule pressure, life-history traits of the invader, and abiotic characteristics of the invaded environment. Most successful invaders have been introduced in high numbers, and at multiple locations, highlighting the importance of propagule pressure (Holle and Simberloff, 2005; Lockwood et al., 2005). Further, the most successful invaders often have generalist habitat and feeding requirements, high rates of dispersal, flexible life history strategies, and high growth and reproduction rates (Peterson, 2003; Simon and Townsend, 2003). Such traits allow invasive species to thrive in a wide range of environments, and to overcome resistance to invasion via competitive and predation pressure exerted by the native community (Levine et al., 2004; Derivera et al., 2005). In addition, an introduced species is more likely to be successful if the invaded environment has abiotic characteristics that meet the species' habitat requirements (Peterson, 2003; Mau-Crimmins et al., 2006).

Among abiotic habitat characteristics affecting the success of aquatic invasive species in river systems, one of the most important is a hydrologic regime that matches that of the invasive species' native range (Moyle and Light, 1996; Fausch, 2008). For instance, invasion success of

brown trout (*Salmo trutta*) and rainbow trout (*Oncorhyncus mykiss*) in streams across the species' introduction range has been attributed to an interaction between the timing of flood events and spawning activity (Moyle and Light, 1996; Spina, 2001). Further, several studies suggest that the distribution of invasive species in California streams may be best explained by interactions between life history strategies of invaders and the timing and magnitude of peak flow events, rather than biotic resistance by the native community (Moyle and Light, 1996).

Stream flow also interacts with geomorphology to influence spatial and temporal differences in habitat structure, including substrate, depth, and velocity. The most successful aquatic invasive species demonstrate life histories and physical traits which benefit from this habitat structure (Schlosser, 1990). In the Colorado River Basin, changes in habitat structure due to flow modifications have created new habitat niches that have been successfully invaded by a number of species which are comparably weaker swimmers and generalist feeders compared to native species (Olden et al., 2006). In addition fish life history strategies in the United States and Australia exhibited similar patterns along gradients of hydrologic variability (Olden and Kennard, 2010). More dynamic processes, such as sediment and nutrient transport, are difficult to quantify but may also shape habitat for aquatic invasive species (Montgomery et al., 1999; Jeffries, 2000).

Brown trout (*Salmo trutta*), one of the world's worst invasive species (Lowe et al., 2000; McIntosh et al., 2011), demonstrates all of the characteristics of a successful aquatic invader. High propagule pressure affects the distribution of brown trout within its introduced range, ranging from California (Moyle and Marchetti, 2006) to Newfoundland (Westley and Fleming, 2011). Brown trout was first introduced outside its native range of Eurasia in 1852 and, since this time, the species has successfully invaded at least 24 countries (Elliott, 1994). Many streams where brown trout has successfully established exhibit similarities in geomorphology and hydraulics to habitat in the species' native range (Lamouroux et al., 2002). Studies conducted in both the species native and introduced range show that brown trout is a habitat generalist that is

able to shift its use of depth and water velocities when conditions change (Heggenes, 2002; Ayllon et al., 2011). Brown trout also exhibit high plasticity in life-history traits, growth, and reproductive rates (Klemetsen et al., 2003). This generalist strategy extends to feeding behavior. Although most salmonids are opportunistic carnivores, brown trout's ability to shift its diet in the presence of changing prey resources may exceed that of other resident-stream salmonids. In several studies, brown trout have demonstrated the capacity to shift from a diet composed exclusively of invertebrates to a diet comprised largely of fish (L'Abée-Lund et al., 1992; McHugh et al., 2008). Brown trout invasion success in several cases has been attributed to a shift to piscivory, which results in increased growth and overall production (Townsend and Crowl, 1991; Macchi et al., 2007).

Similar to other aquatic invaders, brown trout invasion success is linked to physical changes in hydrology and geomorphology that occur in river networks. In many river systems, brown trout are fall spawners and their eggs and fry are still in the gravel during flood events. As a result, brown trout fry and eggs are susceptible to streambed scour and displacement (Spina, 2001; Wood and Budy, 2009). As such, close relationships have been documented between the population dynamics of young brown trout and flood timing and magnitude. Further, in streams across the species' native range, the abundance of young-of-the-year brown trout is low in years following high-discharge events (Cattaneo et al., 2002; Lobon-Cervia, 2004). Such patterns also occur in systems within the species' introduced range (Elliott, 1976; Ottoway et al., 1981; Jensen and Johnsen, 1999). For example, scouring of brown trout eggs and their presence in drift nets suggests high mortality within streams in England characterized by frequent flood events (Ottoway et al., 1981). Patterns of scour and fill can vary widely throughout a reach and temporarily during a flood event, affecting the depth to which scour occurs (Lisle, 1989). Also, salmonids may select areas of low scour for spawning (Montgomery et al., 1996). Therefore,

potential effects of streambed scour on early-life stages of salmonids in the gravel will depend on these patterns of scour and fill, as well as spawning site selection.

The availability of spawning habitat, and specifically gravel availability, may also affect the distribution and invasion success of brown trout. Several studies have highlighted the potential influence of spawning habitat on adult trout abundance (Knapp et al., 1998; Petty et al., 2005; Hudy et al., 2010). For example, in the Kern River, California, adult abundance of California golden trout (*Oncorhynchus mykiss aguabonita*) is closely linked to spawning gravel availability (Knapp et al., 1998). The importance of spawning gravels in structuring the spatial distribution of brown trout densities, however, may depend on the dispersal distance of fish to and from spawning gravels. Using genetic markers, Hudy (2010) demonstrated that proximity to spawning gravels was an important factor influencing the distribution and population structure of largely immobile brook trout throughout a Pennsylvania watershed. Although a similar study has not been conducted for brown trout, Beard and Carline (1991) observed that spawning gravel availability was more important than other habitat factors in influencing brown trout distributions. While some brown trout move relatively long distances to spawn (Meyers et al., 1992; Burrell et al., 2000), in many systems brown trout are largely immobile (Young et al., 1997; Budy et al., 2008). Therefore, the importance of spawning gravels to adult distributions may vary by system.

When brown trout establish high densities, they often aggressively outcompete other stream-resident salmonid species, causing the other species to shift to less suitable habitat conditions (Gatz et al., 1987; Hasegawa et al., 2006). Such shifts in habitat in the presence of brown trout have been observed across several salmonids, including rainbow trout, brook trout (*Salvelinus fontinalis*), masu salmon (*Oncorhynchus masou*), white-spotted char (*Salvelinus leucomaenis*), and cutthroat trout (*Oncorhynchus clarki*). In one such study, native brook trout in a Michigan stream chose resting positions with more favorable water velocities and canopy cover after brown trout were removed (Fausch and White, 1981). Less suitable habitat conditions,

selected by other trout species in the presence of brown trout, are often less profitable in terms of the amount and energetic-quality of prey. As evidence for this, the presence of brown trout resulted in a shift in the feeding niche of Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*) in experimental enclosures (Shemai et al., 2007). In this study, cutthroat consumed more terrestrial food sources in the presence of brown trout, which contained less energy than their preferred food sources. In addition, brown trout in sympatry with cutthroat trout exhibited more aggressive behavior, ate more, and exhibited higher growth rates than when in allopatry (Shemai et al., 2007). Similarly, brown trout growth and condition have been shown to be similar, if not higher ,when in sympatry with native Bonneville Cutthroat trout (*O. clarki Utah)* compared to in allopatry (McHugh and Budy, 2005).

As a predator, brown trout may also have widespread impacts on native communities and ecosystems. However, despite the potential negative effects of brown trout predation on species and whole communities, studies of the impacts of brown trout predation are rare compared to studies focused on competitive interactions. The most comprehensive research on the predatory effects of brown trout on native communities has been conducted in New Zealand (Townsend and Crowl, 1991; Flecker and Townsend, 1994; McIntosh et al., 1994). In some New Zealand streams, native galaxid fish are now restricted to headwaters upstream from waterfalls, where they can avoid predation by brown trout (Townsend and Crowl, 1991). In places where brown trout and native galaxids do co-exist, galaxids exhibit fewer predation attempts (Edge et al., 1993). Likewise, the behavior of stream invertebrates is altered in the presence of brown trout, which feed more at night and spend less time on the surface of rocks during the day (McIntosh and Townsend, 1996). In addition to these effects on individual species, the impacts of brown trout predation may cascade through stream ecosystems. For instance, the presence of brown trout has contributed to lower densities and smaller sizes of macroinvertebrates in New Zealand streams and elsewhere, which has led to lower consumption of algae by macroinvertebrate

grazers and higher algal biomass (Flecker and Townsend, 1994; Stenroth and Nyström, 2003). While effects of brown trout predation in New Zealand have been well-documented, their predatory impact in other geographic areas remains largely unknown and based on anectodal evidence. A better understanding of physical factors that control brown trout distributions, and the resulting impact of brown trout to native communities, could inform management efforts in stream systems where brown trout have been introduced.

Project Goals

Although numerous studies highlight abiotic and biotic factors controlling brown trout invasion success, few efforts (with the exception of a series of New Zealand studies) have systematically evaluated the contributions of multiple factors to brown trout invasion success within the same geographic area. However, on the Logan River, Utah, a series of studies have been designed to isolate the most important abiotic and/or biotic factors influencing invasion success, and ramifications for the invaded community (de la Hoz Franco and Budy, 2005; McHugh and Budy, 2005; Wood and Budy, 2009). Results of long-term surveys show that brown trout densities decrease with distance upstream while, conversely, native Bonneville cutthroat trout densities increase with distance upstream (de la Hoz Franco and Budy, 2005).

While competition with brown trout may explain the absence of cutthroat trout from downstream reaches, past research suggests that the absence of brown trout from upstream reaches may due to abiotic factors. Because upstream portions of the river exhibit colder water temperatures than downstream portions, several studies have focused on how temperature-related factors may influence the distribution. In one such study, the relative growth of brown trout and cutthroat was investigated in experimental enclosures at reaches encompassing a range of elevations and temperatures on the river, and in sympatry and allopatry (McHugh and Budy, 2005). In these experiments, brown trout grew faster than cutthroat at colder, upstream reaches,

in both sympatry and allopatry. In other research efforts, Wood and Budy (2007) investigated the survival of eggs and fry of brown trout in cold winter conditions. Even though survival was lower in some high-elevation, upstream sections compared to in downstream sections, survival was not low enough to explain a decrease in brown trout densities with distance upstream. Currently, ongoing research is being conducted to evaluate whether biotic resistance by cutthroat trout may contribute to low densities of brown trout at higher elevations (Saunders, personal communication).

As part of this larger effort to determine factors affecting the longitudinal distribution of brown trout, and associated ramifications for the native aquatic community on the Logan River, my dissertation research had the following objectives: 1) Investigate how changes in hydro-geomorphic characteristics on the Logan River affect patterns of spawning gravel scour at different spatial scales, and whether patterns of scour could contribute to the decreasing abundance of brown trout along a longitudinal gradient of the Logan River, 2) Evaluate the relative influence of gravel availability versus other abiotic factors in determining the spatial distribution of redd densities along this longitudinal gradient, and 3) Determine abiotic conditions that limit a potential prey resource, the native mottled sculpin, and the potential for brown trout predation on sculpin at reaches throughout the Logan River watershed.

Chapter 1

In chapter 1, I first select and describe geomorphic characteristics of study reaches along a longitudinal gradient of the Logan River. Second, based on egg burial depths and scour depths, I determine whether spawning gravels on the Logan River were likely to be scoured during flood events in 2009 and 2010, which represented typical spring floods. Third, I investigate whether brown trout spawn in local areas of transport capacity as reach potential for spawning gravel entrainment increases, in order to potentially minimize spawning gravel scour. Next, I estimate

whether scour depths are affected by estimates of entrainment potential occurring at the sub-reach, reach, or broad spatial scales. Finally, based on these results, I discuss the potential contribution of scour to the distribution of brown trout densities along a longitudinal gradient of the Logan River.

Chapter 2

In chapter 2, I use a Bayesian hierarchical approach to investigate the role of gravel availability versus a suite of abiotic factors in predicting the spatial distribution of redds densities on the Logan River, Utah. I estimate reach-scale gravel availability using field and remote estimates of unit stream power collected at 83 reaches along a longitudinal gradient. I evaluate a range of abiotic predictors that may affect either early-life stages or adults, including those related to propagule pressure, temperature, and physical habitat structure.

Chapter 3

In chapter 3, I first evaluate abiotic factors potentially contributing to the co-occurrence of exotic brown trout and native mottled sculpin. Next, I compile diet data to determine the prevalence and magnitude of brown trout predation on mottled sculpin. I implement a bio-energetic modeling approach to examine the potential for individual and population-level annual predation on mottled sculpin based on reach-scale diet data and temperature measurements. Finally, I discuss the potential impact of brown trout on mottled sculpin and native fishes in general.

Together, these chapters provide insight into how the changing physical template of the Logan River affects brown trout invasion success, and ramifications for an aspect of the native community. This knowledge will inform future research efforts on the Logan River, as well as contribute to a better understanding of how physical factors control brown trout invasion in other river systems where the species has been introduced.

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CHAPTER 2

SCOUR DEPTHS OF BROWN TROUT (*SALMO TRUTTA*) SPAWNING GRAVELS ALONG THE LONGITUDINAL GRADIENT OF THE LOGAN RIVER, UTAH

ABSTRACT

Eggs and fry of brown trout (*Salmo trutta*) are susceptible to scour and displacement during flood events due to the mobilization of streambed gravels. The goal of this research was to determine whether early life-stages of brown trout on the Logan River, northern Utah USA, are susceptible to scour-related mortality. We also evaluated whether changes in hydro-geomorphic characteristics contribute to increases in spawning gravel scour along a longitudinal gradient, which could potentially explain low densities of brown trout observed at high elevations. In 2009 and 2010, we collected data to identify and characterize brown trout spawning locations and used scour chains to measure scour depths at spawning gravels in representative reaches along the longitudinal gradient. We evaluated how local and reach scale patterns of shear stress and broad-scale geomorphic characteristics influenced scour depths. We observed that brown trout preferentially spawned in low shear stress areas of the channel. Therefore, scour depth did not increase with distance upstream. The most downstream reach exhibited some of the highest scour depths, likely due to a lower threshold needed for bed movement caused by lower armoring and potentially greater sediment supply. In general, local estimates of shear stress predicted scour depth better than reach-scale estimates or broad-scale geomorphic trends. We conclude that patterns of spawning gravel scour do not appear to explain the absence of brown trout from high elevations, but that spring floods could influence brown trout densities through the displacement of emerging fry.

INTRODUCTION

Rivers are characterized by spatial and temporal variation in hydro-geomorphic characteristics, affecting availability of habitat for aquatic organisms (Poff et al., 2006). Such variation in hydrology and geomorphology results from broad-scale influences of geology, climate, and topography, as well as finer-scale variation in disturbance and environmental factors (Montgomery, 1999; Rice et al., 2001; Thorp et al., 2006). By developing a better understanding of how habitat availability and ecological processes are influenced by changes in hydrology and geomorphology, we can better explain the distribution of aquatic species within river networks.

The flow regime of rivers, especially hydrologic variability, is a template upon which patterns of species' distribution, life history, and community organization are based (Poff and Ward, 1990; Oberdorff et al., 2001). Floods replenish backwater wetlands, transport woody debris, contribute to sediment transport and deposition, and provide environmental cues for spawning fish (Poff, 1997). Stream flow also interacts with geomorphology to influence spatial and temporal differences in habitat structure. Such factors are commonly used to explain the distribution of biotic communities, including fishes (e.g., Lamouroux and Capra, 2002; Poff and Allan, 1995).

Changes in the physical template are influenced by controls operating at different spatial scales. For instance, watershed-scale differences in flow and sediment regimes are a function of regional climate, geology, and topography. Stream channel morphology and slope are primarily controlled by sediment supply and transport capacity within these regional constraints. At the reach scale, channel morphology is further influenced by local controls such as the location of coarse particles and woody debris. In turn, this channel morphology controls local-scale and microhabitat characteristics including substrate size, nearbed velocity, and flow depth. Physical characteristics occurring at these more local scales are important to fish habitat selection and

many critical ecological processes for aquatic biota. Thus, the types of habitat available within a reach (including the presence of local morphological features) ultimately depend on properties occurring at broader (e.g., river segment or watershed) spatial scales (Frissell et al., 1986).

Spatially contiguous sections of rivers that share similarities in geomorphic characteristics and disturbance regimes have been called "process domains" or "process zones" (Montgomery and Buffington, 1997). The process zone concept and other related paradigms illustrate how physical habitat and resulting ecological processes can exhibit non-linear changes along the longitudinal continuum of rivers, due to changes in broad-scale characteristics of the landscape (Frissell et al., 1986; Thorp et al., 2006). Through identification of such broad-scale characteristics, portions of rivers which share similarities in finer-scale ecological processes may be determined and included in efforts to predict the distribution of species (Wohl, 2010; O'Hare et al., 2011)

Within many systems in the species' native and introduced range, brown trout (*Salmo trutta*) is a fall-spawner with population dynamics that are strongly linked to both geomorphology and hydrology. During the fall spawning period, brown trout select portions of channel for spawning that contain substrates within a preferred size range (Shirvell and Dungey, 1983). Brown trout eggs develop into fry within the gravel during the cold winter period, and the developmental rate and timing of emergence from the gravel depends on stream temperature. In many systems, emergence occurs near the time of spring floods, such that developing brown trout eggs and fry may be susceptible to mortality related to the scouring of spawning gravels (Spina, 2001; Wood and Budy, 2009). Close relationships have been documented between the population dynamics of young brown trout and flood timing and magnitude (Cattaneo et al., 2002; Lobon-Cervia, 2004; Jonsson and Jonsson, 2009). In addition, for streams characterized by frequent flood events, large scour depths and the presence of brown trout eggs in drift nets suggest high mortality of this life stage during flood events (Elliott, 1976).

Even though relationships between discharge and abundance of brown trout are commonly attributed to such scour effects, potential effects of scour are rarely investigated in the field. In addition to affecting inter-annual variation in the survival of early life stages, vulnerability to scour could also vary spatially throughout river networks, ultimately affecting brown trout abundance. Such variability could result from variation in channel morphology, substrate size and configuration, and sediment supply. However, most scour studies are confined to a single reach and not designed to consider the potential for broader-scale patterns (Rennie and Millar, 2000; May et al., 2009).

In this study, we explore whether early life stages of brown trout in the Logan River are susceptible to scour-related mortality during spring flood events, and how changes in geomorphic characteristics influence the spatial distribution of scour along a longitudinal gradient. The distribution of native Bonneville cutthroat (*Oncorhynchus clarkii Utah*) and exotic brown trout on the Logan River have been previously investigated as part of long-term study efforts to assess both the population viability of cutthroat trout and the impact of brown trout to the native fish community. However, previous research has failed to fully identify the mechanisms contributing to the longitudinal distribution of brown trout (de la Hoz Franco and Budy, 2005; McHugh and Budy, 2005; Wood and Budy, 2009). By identifying the factors that limit exotic brown trout abundance in this and other systems, we can inform management efforts to conserve native trout populations in systems which contain brown trout, as well as better predict how brown trout populations will respond to climate change or habitat alteration.

In order to evaluate potential for scour of developing brown trout eggs and fry along a longitudinal gradient of the Logan River, we studied patterns of scour in relation to spawning habitat selection. As part of this research, we asked the following questions:

i) How do reach and substrate characteristics used for spawning by brown trout vary along a longitudinal gradient of the river?

(ii) Could bed scour during typical flood events contribute to mortality of developing brown trout eggs and fry?

iii) How does selection of low shear stress areas for spawning minimize the potential for scour-related mortality?

(iv) How do changes in stream geomorphology, occurring at the local, reach, and process zone scales, affect scour depths along a longitudinal gradient?

METHODS

Study area

The study area is located in the Logan River watershed within the Bear River Range of northern Utah (Figure 2.1). Elevations of the study reaches range from 1536 m at the downstream end up to 2077 m at the most upstream reach (Table 2.1); watershed area of the study reaches ranges from to 82.9 km^2 to 526 km^2. Three major tributaries enter the Logan River within the study area: Beaver Creek (watershed area = 110 km^2), Temple Fork (watershed area = 41 km^2), and Right Hand Fork (watershed area = 65 km^2).

Immediately downstream from the study area is a series of three small dams, named from downstream to upstream as First Dam, Second Dam, and Third Dam. Because of the influence of these dams on the natural hydrology of the river, we designated the downstream portion of the study area as the reach located immediately upstream of the backwater of Third Dam. Our chosen study area encompasses patterns of brown trout density that occur longitudinally on the unregulated portion of river (Budy et al., 2008). The backwater of Third Dam supports some of the highest densities of brown trout spawning and brown trout adults in the study area, whereas the uppermost reaches of the study area--Franklin and Bridge--contain no brown trout.

Peak discharge on the Logan River typically occurs in May and June, although the annual

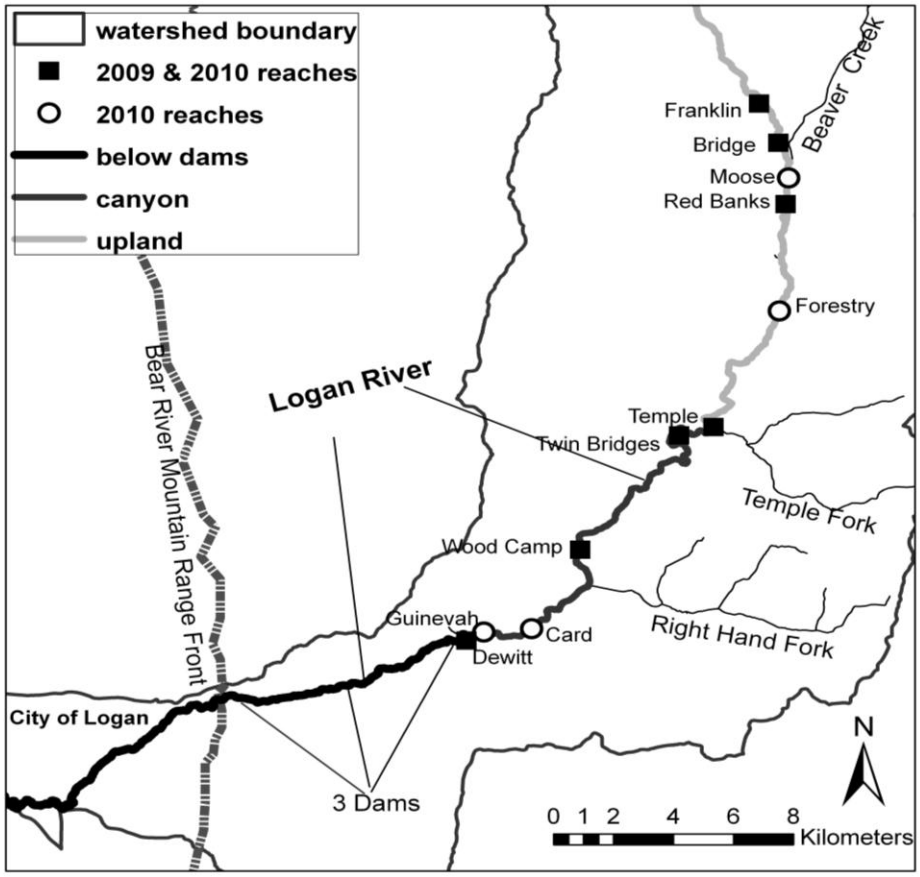

Figure 2.1 Locations of study reaches.

peak has occurred as early as April and occasionally in fall during droughts years. The river has a relatively low peak-to-base flow ratio, because infiltration into the abundant limestone in the watershed dampens the magnitude of snowmelt runoff and increases the magnitude of baseflows. The 2-yr recurrence flood, measured at USGS gage 10109000 (located approximately 7 km downstream from the study area) is approximately 25.95 m^3/s for the period of record (1902-2008) and the mean daily flow is approximately 6.7 m^3/s.

Channel morphology varies along the length of the river due to differences in geology and topography. Upstream reaches in the study area are generally characterized by a relatively

unconfined canyon and coarse-grained glacial deposits. Downstream reaches are confined within a bedrock canyon and dominated by more varying substrate composition, due to inputs of both large and small substrates from hillslopes and canyon walls. The entire study area is characterized by a similar flow regime. Therefore, changes in the physical template are primarily caused by interactions between hydrology and geomorphology, which result in spatial variation in shear stress and substrate size.

Reach selection and characterization

We selected study reaches to represent the range of geomorphic conditions present on the Logan River. We characterized the morphology of each reach using the scheme developed by Montgomery and Buffington (1997) (Table 2.1). Study reaches were approximately 20 channel widths in length. We established the Dewitt, Woodcamp, Twin Bridges, Temple, Redbanks, Bridge, and Franklin 2 reaches in 2009. We added Guinevah, Card, Forestry, and Moose reaches in 2010 to capture a wider range of geomorphic conditions, including steeper gradients (Figure 2.1).

For each reach, we estimated the reach-scale median particle size (D_{50}); median spawning gravel substrate size ($D_{50\text{-}spwn}$); reach average total boundary shear stress during baseflow (τ_{base}), during the peak discharge of the 2009 flood event (τ_{09}), and during the peak discharge of the 2010 flood event (τ_{10}); critical shear stress of the D_{50} (τ_{cr}); and reach entrainment potential of the D50 during the 2010 flood event (ET_{10}) as described below (Table 2.1).

We separated each reach into morphological units characterized by changes in slope and substrate, and we estimated the D_{50} of each study reach by proportionally weighting the D_{50} of each morphological unit by the area of each unit within the reach (Kondolf, 1997). We estimated D_{50} of each morphological unit using 100-point counts (Wolman, 1954).

Table 2.1. Reach Characteristics

Reach	reach type	elev-ation(m)	gradient	D_{50} (mm)	$D_{50\text{-}spwn}$ (mm)	τ_{base} (Pa)	τ_{09} (Pa)	τ_{10} (Pa)	ET_{10}
Dewitt	pool-riffle	1536	0.003	45	18	17	33	32	0.73
Guinevah	pool-riffle, bedrck	1557	0.006	56	16	47	*	104	1.91
Card	pool-riffle, bedrck	1569	0.014	87	12	69	*	112	1.33
Woodcmp	pool-riffle, bedrck	1611	0.023	125	11	94	147	136	1.12
Twin	pool-riffle, bedrck	1721	0.008	84	9	34	81	76	0.93
Temple	pool-riffle, bedrck	1765	0.012	123	11	82	135	118	0.99
Forestry	plane-bed	1854	0.016	208	10	105	*	150	0.74
Redbanks	plane-bed/step-pl	1972	0.023	144	10	68	151	117	0.84
Moose	plane-bed/step-pl	1982	0.025	119	10	96	*	194	1.68
Bridge	plane-bed/step-pl	2010	0.024	114	10	64	134	109	0.98
Franklin	planebed/cascade	2077	0.028	194	12	109	190	170	0.90

In order to estimate $D_{50\text{-}spwn}$, we performed point counts within spawning gravel patches. We defined a spawning patch as a continuous, concentrated area of observed spawning activity, often containing many nests or redds, located within morphological units characterized by similar slope and width. We performed point counts in two or three spawning patches in each reach and combined observations across patches to obtain $D_{50\text{-}spwn}$. The number of spawning patches varied from two to five per reach, and locations of patches used for spawning did not vary between years. We also estimated the grain size distribution of patches suitable for spawning (based on measurements of velocity, depth, and substrate) within reaches where spawning did not occur (e.g., Bridge and Franklin)

In order to characterize differences in hydraulic conditions, we measured water surface and bed profiles in each study reach during baseflow and flood flow conditions using a Topcon Hiper Pro GPS unit (Topcon, USA). For estimates of flood conditions, we flagged water surface elevations in 2009 and 2010, and surveyed these locations after floods had receded. We

estimated reach-average total boundary shear stress for each reach during baseflow and flood conditions using a form of the DuBoys equation,

$$\tau = \rho_w * g * H * S \qquad (1)$$

where τ is the reach-averaged total boundary shear stress during either baseflow, 2009, or 2010, ρ_w is the density of water (kg/m^3), g is gravitational acceleration (m/s^2), H is the appropriate reach average flow depth (estimated at the midpoint of the reach), and S is the appropriate average reach slope (based on the longitudinal survey of water surface elevations) (Figure 2.2). We estimated the critical shear stress of the D_{50} (τ_{cr}) using a high estimate of the Shields number (τ^*=0.060, due to the extensive armoring that we observed at most reaches) and the median grain size:

$$\tau_{cr} = \tau^* D_{50}(\rho_s - \rho_w)g \qquad (2)$$

where ρ_s is sediment density (kg/m^3). We calculated entrainment potential for each reach during the 2010 flood (ET_{10}) by dividing the 2010 estimate of flood shear stress by the critical shear stress (τ_{10}/τ_{cr}). However, based on tracer rock experiments suggesting that partial mobility occurs throughout reaches in the study area, we concluded that mobility of spawning gravels depends on the local spawning gravel D_{50} and not the reach D_{50}. Given the small range of spawning gravel sizes and resulting similarity in critical shear stresses at spawning gravel patches, we estimated reach-scale entrainment potential of spawning gravels as the reach-average total boundary shear stress, τ_{09} or τ_{09}.

Hydrology and fry emergence

We estimated the recurrence of the 2009 and 2010 spring floods from a flood frequency analysis of the instantaneous peak discharge record of USGS gage 1010900, where peak flow measurements have been made since 1896 (102 years total, given twelve missing years). The

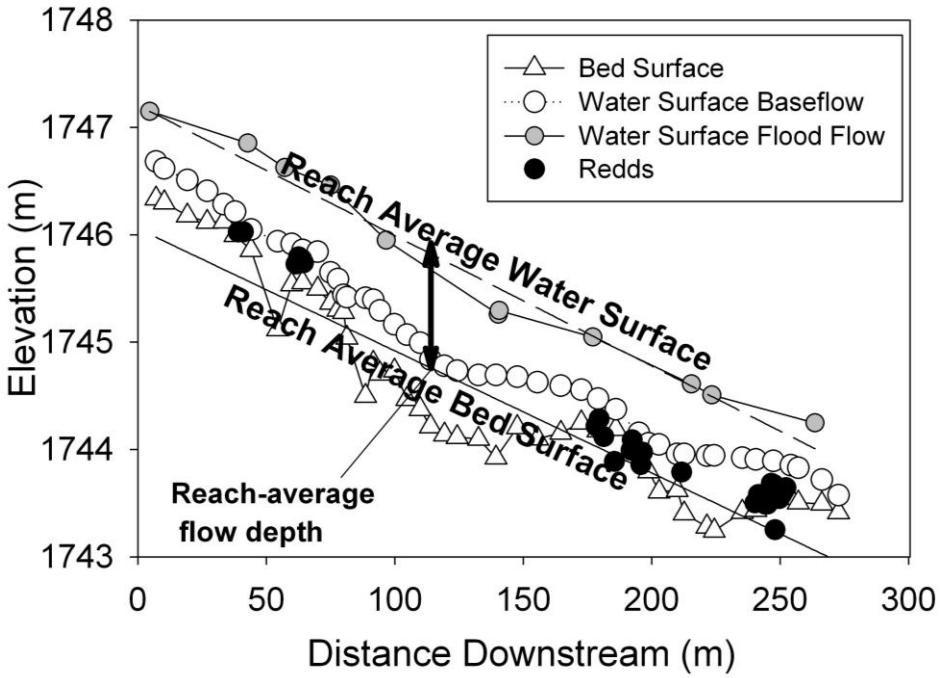

Figure 2.2. Water surface and bed surface elevation profiles were used to estimate reach-average base and flood water surfaces, bed surface, reach-average flow depth, and water surface slope.

three dams located between the study area and the gage have no effect on peak flow, because there is no effective reservoir storage at these impoundments. We also estimated the hydrographs for the two floods from stage-discharge relationships developed for pressure transducers located near the Guinevah, Forestry, and Franklin reaches. (M. Majerova and J. Schmidt, Utah State University unpublished data).

We compared the flood hydrographs to estimates of brown trout peak emergence developed from temperature measurements collected in each reach using HOBO temperature loggers. We estimated peak emergence based on hourly averages of temperature estimates (Wood and Budy, 2009).

Egg burial versus scour depths

We used scour chains to estimate the depth of scour following spring floods in spawning gravel patches in each reach (2009 and 2010). To insert scour chains, we used a method similar to Nawa and Frissell (1993). In 2009, one scour chain was inserted in a representative redd in each gravel patch where we previously observed the highest densities of spawning activity. In 2010, we increased the number of scour chains to include every spawning gravel patch in a reach, in order to encompass a wider range of geomorphic conditions. We inserted scour chains immediately adjacent to an actual redd in the patch. We determined the amount of scour occurring during the flood event by subtracting the length of chain protruding horizontally from the gravel following the flood event (in July of each year) from the amount of chain protruding approximately one week prior to the flood event. Scour chains relocated in 2010 also included those previously inserted in 2009. Since we observed no spawning activity in two reaches above the elevational limit of brown trout occurrence (e.g., Bridge and Franklin), we inserted scour chains in patches of gravel that exhibited substrate size, velocity, and depth characteristics used by spawning brown trout in other reaches.

We used egg burial depths to approximate the depths of developing eggs and fry still in the gravel during spring floods. Although we observed that most of the developing brown trout were at the fry stage prior to the flood, fry depths were difficult to sample immediately before flood events due to rising flood waters. DeVries (1997) suggested that egg burial depths could be used as a conservative estimate of fry depths. We confirmed this assumption by excavating a subset of redds immediately prior to the flood, and by verifying that a large proportion of fry could be found at depths similar to egg burial depths.

We estimated fry depths from egg burial depths conducted following spawning in either 2009 or 2010. Redds were chosen downstream of scour chains to avoid having an influence on scour depth estimates. Prior to excavation, we used a Topcon AT-G4 Autolevel (Topcon, USA)

to make a series of bed elevation measurements at specific portions of the redd. After we measured the bed surface, we used a shovel to remove layers of sediment within each portion of the redd until we located a pocket of eggs. We then surveyed the elevation of the eggs, and we estimated egg burial depth as the difference between the initial elevation of the portion containing the eggs and the elevation of the eggs.

We used an ANOVA to compare scour and egg burial depths between years and between scour chains inserted in 2009 compared to 2010. In this analysis, we considered separately the scour chains inserted in 2009, because the removal of sediment following the 2009 flood may have affected scour depths at the same chains in 2010.

Spawning habitat selection

We test three hypotheses regarding local selection of spawning patches by brown trout: (1) patches used for spawning have similar values of local shear stress, regardless of increases in reach shear stress (2) brown trout preferentially choose patches for spawning where the water surface flattens as the flow rises to flood stage (i.e., rising limb), which may minimize entrainment of spawning gravels; and (3) brown trout preferentially use channel margins for spawning as reach shear stress increases.

To test our first hypothesis, that brown trout preferentially select areas of low local shear stress for spawning as reach shear stress increases, we compared estimates of τ_{10} to estimates of shear stress at spawning patches surveyed following spawning in 2010. We used equation 1 to estimate shear stress at spawning gravel patches (τ_{loc}); however, we used average height and slope over each patch instead of reach-averaged values for this calculation (Figure 2.3).

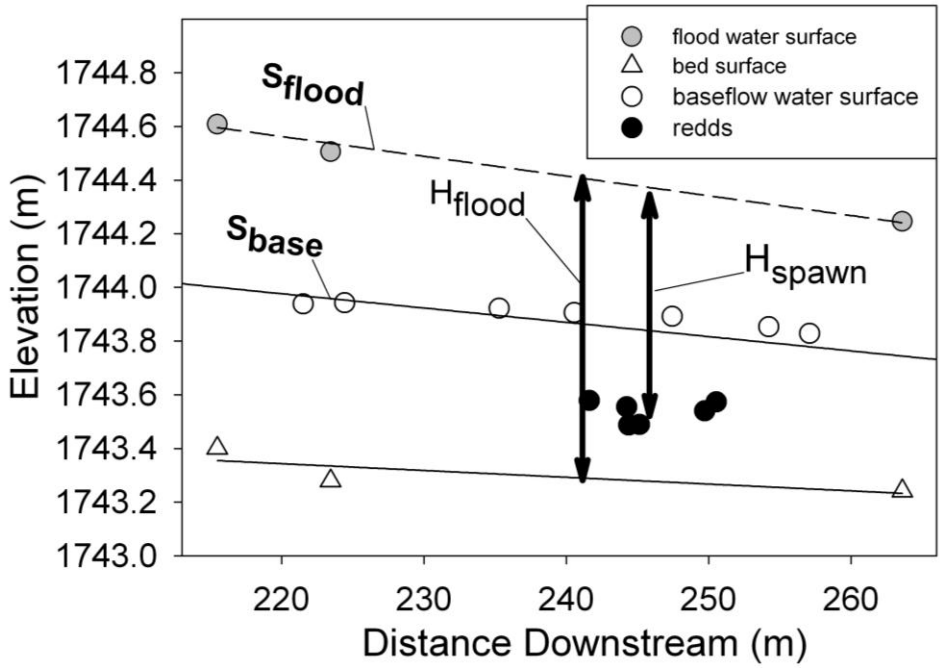

Figure 2.3. The local water surface slope was estimated over each spawning gravel patch containing redds during baseflow (S_{base}) and floodflow (S_{flood}), and flow depth was estimated both over each patch (H_{spawn}) and over the center of the channel (H_{flood}).

To test our second hypothesis, that brown trout select for portions of channel that flatten as reach shear stress increases, we compared τ_{10} to the proportional change in slope at gravel patches from baseflow to floodflow in 2010 (i.e., "flattening ratio") whereas:

$$Flattening\ Ratio = (S_{base}-S_{flood})/S_{flood} \quad (3)$$

Values > 0 indicate flattening of the water surface during the rising limb of the flood hydrograph, and values < 0 indicate steepening during the rising limb (Figure 2.3). We did not include the dam backwater zone or Dewitt reach in our analysis, because the precision of the GPS was not high enough to detect changes in slope within this low-slope reach.

To test our third hypothesis, that brown trout select for low water depths indicative of channel margins, we compared estimates of τ_{10} and depths used for spawning in relation to thalweg depths, whereas

$$Proportion\ Thalweg\ Depth = (H_{spawn}/H_{flood}) \quad (4)$$

,with values indicating the proportion of thalweg depth occurring at spawning locations (Figure 2.3).

We used a series of linear regression models to test our hypotheses regarding changes in τ_{loc}, flattening ratio, and proportion thalweg depth with increases in τ_{10}. We performed all analyses using the R statistical program (R Core Development Team, 2011).

Influences of the physical template on patterns of scour along a longitudinal gradient

We used a linear regression model to test whether scour depths increased with distance upstream from Third Dam (the most downstream reach in the study area). We also tested whether scour depths increased with increases in τ_{loc} and τ_{10} occurring within spatially contiguous process zones.

We delineated process zones using data derived from longitudinal surveys, digital elevation models (DEMs), and geologic maps. Using a geologic map of the study area, we identified dominant lithotopo units, or areas with similar topography and geology (Montgomery, 1999). We then used trends in valley width, slope, and unit stream power to define process zones within these lithopo units (Montgomery, 1999; Wohl, 2010; Polvi et al., 2011). We estimated slope, confinement, and unit stream power for 200-m long reaches located along previously surveyed portions of the river (Chapter 3). We calculated reach slope as the difference between the maximum and minimum water surface elevations of each reach divided by reach length, where elevations and lengths were estimated from surveys conducted with the Topcon GPS unit.

We estimated valley confinement by determining the valley width at an elevation 4 m above the channel centerline of each reach using a 10-m DEM of the study area (Townsend et al., 2004). We estimated unit stream power (Ω) during bankfull floods for each reach as:

$$\Omega = \frac{\gamma * Q_{bf} * S_w}{w} \qquad (5)$$

where γ is the unit weight of water (9800 N/m^3), Q_{bf} is estimated bankfull discharge (m^3/s), S_w is water surface slope of the reach (unitless), and *w* is bankfull width(m). We estimated bankfull discharge at each reach from a relationship between watershed area and bankfull discharge developed from measurements at pressure transducers and/or stage height recorders located throughout the watershed.

We used a mixed model toevaluate the relative influence of τ_{loc}, $\tau_{10,}$, and process zone on scour depths. For this analysis, we considered reach to be a random effect nested within process zone. We considered τ_{loc}, τ_{10}, and process zone to be fixed effects. In contrast to our other analyses, this analysis was conducted using Statistical Analysis Software. We also used scatterplots and linear regression models to investigate the strength and slope of the relationship between estimates of shear stress and scour depth within our process zones; low sample size prevented a statistical evaluation of interactions.

RESULTS

Hydrology and fry emergence

At USGS gaging station 10109000, the peak discharge of the snowmelt flood in 2010 (25.6 m^3/s) was only 12% less than in 2009 (peak discharge = 29.2 m^3/s), but the duration of the 2010 flood was much shorter and occurred later in the year (Figure 2.3, Figures 2.3A and 2.3 B). The 2009 peak occurred on May 25, whereas the 2010 peak flood did not occur until June 7.

Based on the flood frequency analysis of the gage station data, the recurrence of the 2009 instantaneous peak discharge was 2.4 years, and the recurrence of the 2010 peak discharge was 1.8 years. Discharge exceeded baseflow conditions for a total of 153 days after the flood began in 2009, whereas in 2010 baseflow conditions were exceeded for only 134 days. Also, in 2009, the discharge remained within 10% of peak flow for 20 days, whereas in 2010 the discharge remained within 10% of peak flow for only 7 days. In both 2009 and 2010, we predicted that 50% of fry at low elevations emerged by one week prior to the peak flood event, while 50% fry at higher elevations emerged during the peak of the flood (Figures 2.4A and 2.4B).

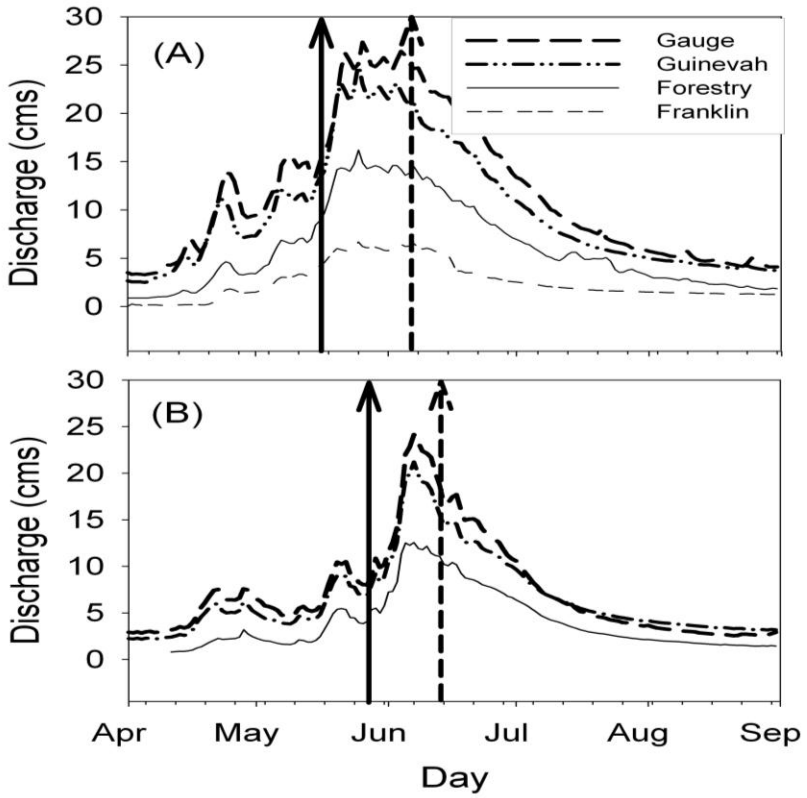

Figure 2.4. Discharge estimates at the USGS gaging station 1019000 and three pressure transducers located at low (Guinevah), medium (Forestry) and high elevations (Franklin) on the Logan River in 2009 (A) and in 2010 (B). No data was available for the Franklin transducer in 2010. Arrows indicate the predicted time of peak emergence in each year for reaches downstream of Temple Fork (solid) and upstream of Temple Fork (dashed).

Egg burial versus scour depths

Brown trout on the Logan River deposited their eggs at shallower depths than the 8-cm reported average (DeVries, 2002). Mean egg burial depth for all sites was 6.1 cm (95% CI=+/- 1.04), and median egg burial depth was 6.8 cm. We found brown trout eggs in 20 of the 36 excavated redds.

Scour depths at both previously-inserted and newly-inserted scour chains in 2010 were significantly less than scour depths in 2009 (Figure 2.5, $F_{3,66}$=25.58, p<0.001). Scour depths in 2009 did not significantly differ from average egg burial depths, but scour depths in 2010 were significantly shallower than egg burial depths. In 2010, scour depths at scour chains inserted prior to the flood did not differ significantly from depths inserted prior to the 2009 flood. On the Temple Fork, Dewitt, and Woodcamp reaches, we were unable to relocate one scour chain each in 2010 that was previously inserted in 2009.

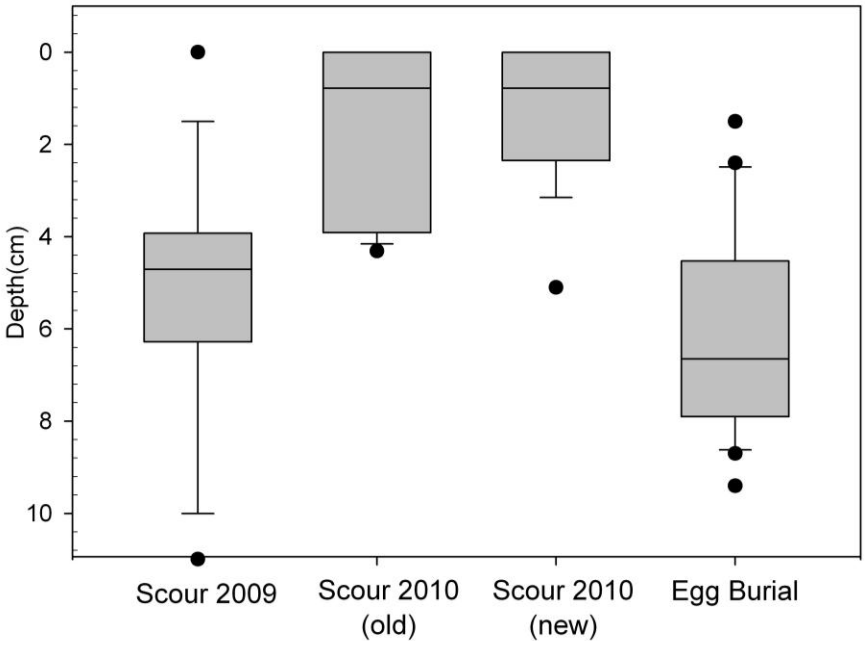

Figure 2.5. Scour depths in 2009 and 2010 in relation to egg burial depths. "Old" refers to scour chains that we inserted prior to the 2009 flood but were re-checked in 2010, while "new" refers to scour chains that we inserted before the 2010 flood.

Spawning habitat selection

Brown trout preferentially selected areas of low local shear stress (τ_{loc}) for spawning. Although shear stress (τ_{loc}) at spawning areas generally increased with increases in reach shear stress (τ_{10}) (Figure 2.6A, F_{29}=46.31, p=<0.0001, R^2=0.570, n=30), τ_{loc} at spawning areas was less than proportional (1:1) to τ_{10}. As we hypothesized, the number of flattening sections (flattening ratio > 0) used for spawning increased as τ_{10} increased; however, the trend was not significant (Figure 2.6 B, F_{21}=0.494, p=0.489, R^2=0.022, n=24). The proportion of thalweg depth used by brown trout for spawning declined as τ_{10} increased, although the decrease was not significant (Figure 2.5 C, F_{29}=1.646, p=0.210, R^2=0.021, n=30). We observed that only 13% of the spawning patches evaluated demonstrated depths at spawning within 10% of the thalweg depth, suggesting a consistent preference for shallower depths present at channel margins.

Influences of the physical template on patterns of scour along a longitudinal gradient

Scour depths at spawning gravels were consistently lower than egg burial depths along a longitudinal gradient. Scour depths did not significantly increase with distance upstream in 2009 (Figure 2.7A, $F_{1,17}$=1.855, p =0.191, R^2=0.110) or 2010 (Figure 2.7 B, $F_{1,30}$=0.654, p= 0.425, R^2=0.045).

Based on our estimates of slope, valley confinement, and stream power, we delineated three broad hydro-geomorphic zones located along a longitudinal gradient of the river (Figure 2.8,A-D). These unique hydro-geomorphic zones exhibited the following general characteristics, and were located from downstream to upstream: (1) a reservoir backwater zone that was partially confined (valley width = 74 m) with low channel slope (0.003), consisting of one reach located

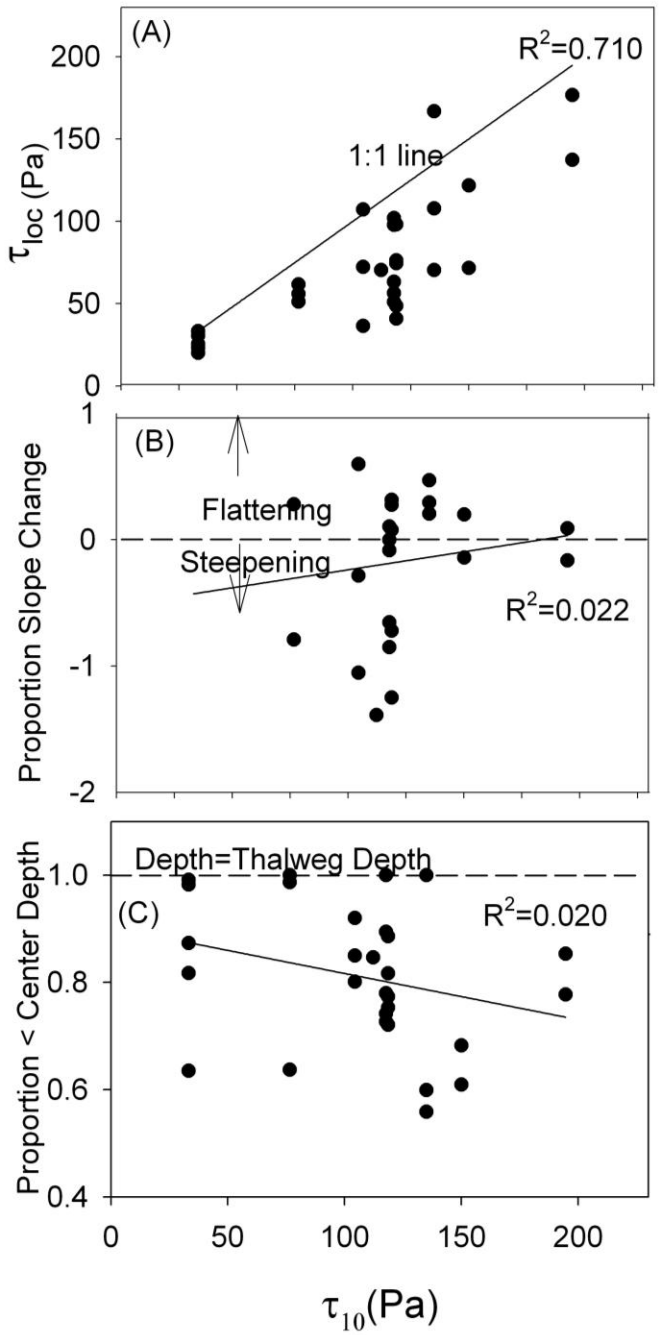

Figure 2.6 Characteristics of areas chosen for spawning by brown trout in relation to τ_{10}, including: (A) local shear stress, τ_{loc} (B) the proportion slope change at spawning gravels during flood flow compared to base flow and (C) the relative flow depth at spawning gravels compared to thalweg depth.

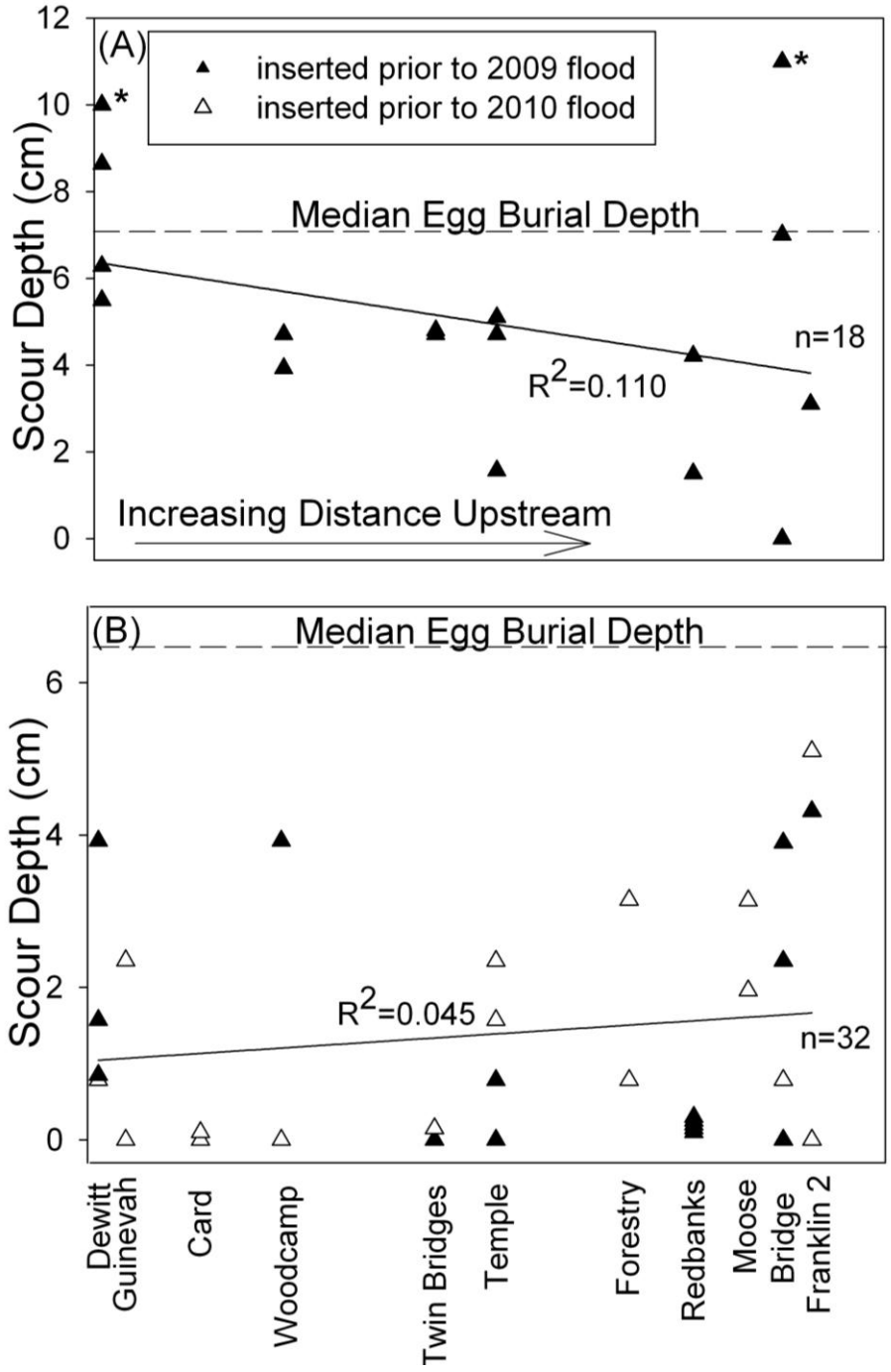

Figure 2.7. Scour depths at scour chains following the 2009 (A) and 2010 (B) flood events. The relative distance between reaches reflects actual distance. An asterick (*) denotes that LWD located directly upstream of the scour chain may have influenced scour estimates. Note that the scale of the x axis differs for 2010 compared to 2009.

immediately upstream of the backwater of Third Dam; (2) a canyon zone that was confined (valley width = 38 +/4.75) with moderately high channel slope (0.007-0.023); and (3) an upstream zone that was partially confined (valley width = 72 +/- 9.1) with high slope (0.017-0.028. The study area is located within two dominant lithotopo unit, coinciding with the transition from the upstream zone to the canyon zone (Figure 2.8).

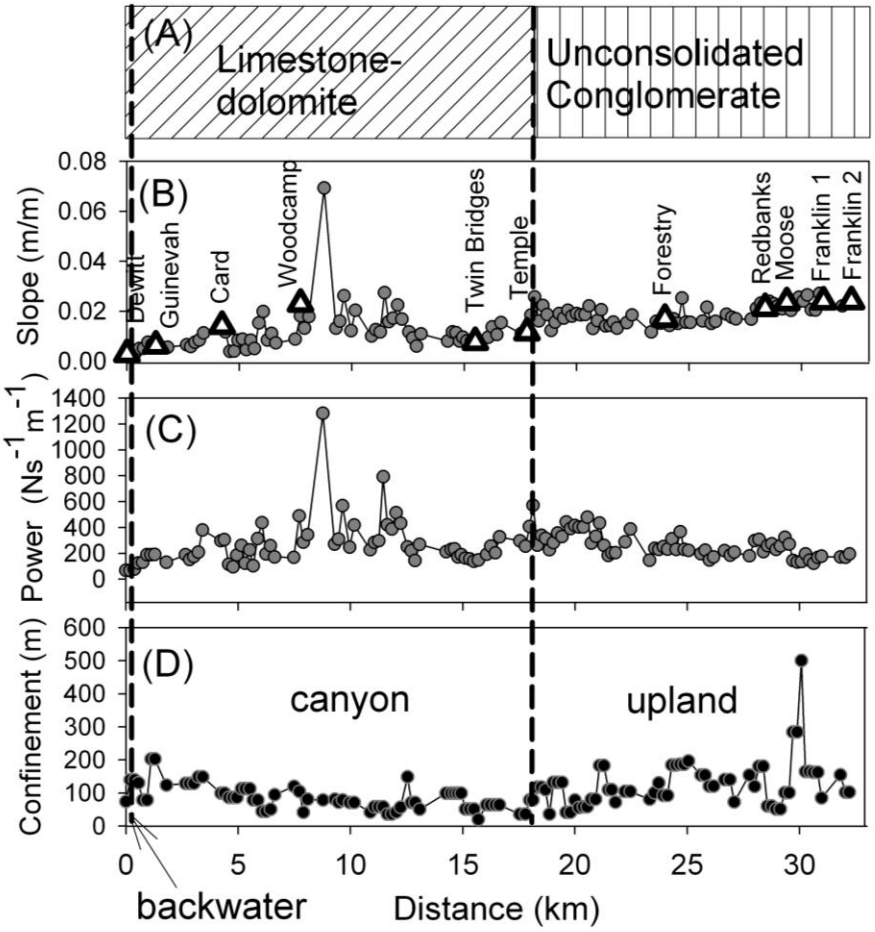

Figure 2.8. Physical characteristics used to determine broad-scale hydro-geomorphic zones along a longitudinal gradient of the study area, including (A) Litho-topo units in the study area. (B) Slope with increasing distance upstream. (C) Unit stream power with increasing distance upstream (D) Confinement with increasing distance upstream (higher values indicate less confinement). Note: the high slope reach upstream of the Woodcamp study reach is the location of a steep waterfall feature on the river.

Our measure of local shear stress (τ_{loc}) showed a strong, positive relationship with scour depths. We found that τ_{loc} significantly predicted scour depth whereas our reach shear stress (e.g., τ_{10}) and broad-scale hydro-geomorphic zones did not (Table 2.2). In addition, scatter plots illustrated a strong, positive relationship between τ_{loc} and scour depth (Figure 2.9A).

Table 2.2 Outcome of mixed model evaluating the influence of τ_{loc}, τ_{10}, and process zone on scour depths.

Effect	**Numerator DF**	**Denominator DF**	**F-Value**	**P-value**
τ_{10}	1	13.79	1.32	0.269
τ_{loc}	1	24.2	20.6	0.0001
process zone	2	8.434	1.68	0.243

Scatterplots revealed a strong pattern which could not be detected by our statistical analysis (i.e., low sample size). Scour chains in the backwater hydro-geomorphic zone exhibited relatively high scour depths at lower levels of shear stress than those found in the canyon and upstream zones (Figure 2.9A). The slope of the relationship between τ_{loc} and scour depth did not differ greatly between zones (1 cm change in scour depth with a 21.2 change in τ_{loc} for the canyon zone, and 1cm change in scour depth with a 15.8 change in τ_{loc} for the upstream zone) but was higher in the canyon zone. Scour depth varied significantly and positively with τ_{loc} in both the canyon zone (Figure 2.9A, $F_{1,10}$=18.44, p=<0.001, R^2=0.613, n=12) and the upstream zone (Figure2.9A,$F_{1,14}$=10.37,p=0.006, R^2=0.384,n=16).

At the reach scale, scour depth exhibited a weak, positive relationship to estimates of shear stress (Figure 2.9B). We were not able to evaluate how scour depths varied with τ_{10} for the

backwater zone, because this zone was comprised of only one reach. However, scour was comparably high for the reach in this zone, despite a low measure of τ_{10}. Scour depth did not vary significantly with reach shear stress within the canyon zone (Figure 2.9B,$F_{1,10}$=1.91, p=0.197, R^2=0.076,n=12) or the upstream zone (Figure 2.9B,$F_{1,14}$=3.908, p=0.07, R^2=0.162,n=16).

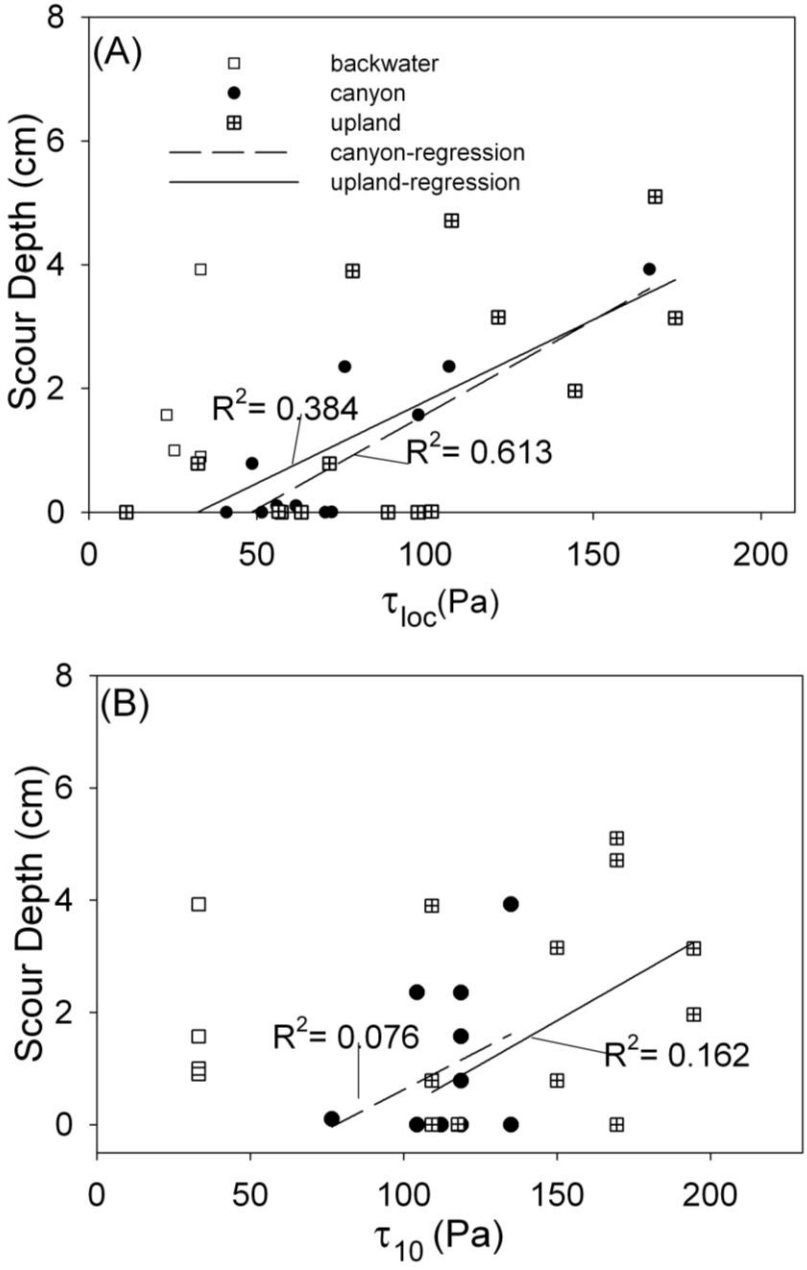

Figure 2.9. Scour depth in relation to τ_{loc} (A) and τ_{10} (B) , with linear regression lines illustrating trends in scour depth.

DISCUSSION

We evaluated how scour depths of brown trout spawning gravels varied along a longitudinal gradient of the Logan River, in relation to brown trout spawning gravel selection patterns and changes in hydro-geomorphic characteristics occurring at the local and reach scale. We found that the potential for displacement of developing brown trout fry due to scour was generally low across the study area during two flood years at or near bankfull. Reach-scale estimates of shear stress were not a significant predictor of scour depths. Instead, scour depth appeared to be determined by local shear stress at sites chosen for spawning. Scour was minimized because brown trout chose areas with low shear stress for spawning.

Despite the low effects of scour observed, emergence at upstream reaches was closer in timing to the flood event, suggesting the potential for displacement of fry after emergence. We predicted earlier emergence times for higher-elevation sites compared to lower elevation sites in both 2009 and 2010. Using a similar but coarser approach, Wood and Budy (2009) also predicted earlier emergence at low elevations. Our research confirms that the susceptibility of displacement is higher for emerging fry at higher-elevation reaches, but that similar flood timing occurs at sites along the length of the river. Susceptibility to displacement therefore differs across a longitudinal gradient due to differences in emergence timing but not flood timing. Such variation in emergence in this system may affect brown trout population dynamics through variation in recruitment, potentially resulting in lower brown trout densities at higher elevations. For instance, within the native range of brown trout, densities of age-0 brown trout are negatively correlated with the flood magnitude at the time of emergence (Cattaneo et al., 2002; Lobon-Cervia, 2004). We did not investigate such effects on population dynamics in our study, but such trends are currently being evaluated as part of long-term study efforts on the Logan River.

Our results demonstrated that the potential for scour-related-related displacement was minimal because brown trout selected for low shear stress areas which were often in channel margins. We observed that brown trout almost always chose channel margins for spawning, likely because they contain more suitable (i.e., less coarse-grained) substrates. In general, redd site selection by trout may be influenced by more proximate cues such as spawning gravel size, current velocity, flow depth, dissolved oxygen content, and interactions among these factors (Shirvell and Dungey, 1983; Baxter and Hauer, 2000). Preference for these conditions may or may not coincide with areas with low scour (Zimmer and Power, 2006; May et al., 2009). For example, within a low-gradient alluvial channel in Washington, chum salmon preferentially spawned in pool tails, which were highly susceptible to scour (Schuett-Hames et al., 2000). In our study, preferred spawning gravels were generally located in areas of lower shear stress. The dam backwater zone was the only portion of our study area where spawning occurred in the center of the channel, and we attribute this to the presence of preferred substrates. Therefore, the availability of spawning gravels and other suitable abiotic conditions may have contributed to the selection of low-scour sites for spawning.

At most spawning locations, we found that scour depths were generally less than typical brown trout egg burial depths during 2009 and 2010 (e.g., at or near bankfull conditions). Only 17% of scour chains exhibited scour depths greater than average egg burial depths in 2009, and 0% of scour chains in 2010 exhibited scour depths greater than egg burial depths. A number of studies have demonstrated that displacement of eggs is typically unlikely at floods lower than bankfull (Lapointe et al., 2000; May et al., 2009; Shellberg et al., 2011). In a river in Quebec, only 5% of developing eggs were predicted to be displaced during typical spring flood events (Lapointe et al., 2000). In our study, both flood duration and flood magnitude may have influenced scour depths, since the 2010 flood was 12% less in magnitude than the 2009 flood but of shorter duration. Similarly, in mountain streams in Washington, accounting for flood duration

allowed for better prediction of scour depth, as compared to studies that only considered the flood recurrence interval (Konrad et al., 2002; Shellberg et al., 2011).

Our scour depths were generally less than those observed in studies of spawning gravel scour conducted in low-gradient systems where spawning occurs in areas throughout the channel (Montgomery et al., 1996; Rennie and Millar, 2000). In contrast, they are similar to those observed in a coarse-bedded mountain streams in Washington, USA, where spawning occurred in channel margins (Shellberg et al., 2011). Despite the relatively low scour depths that we recorded, our average egg burial depth (~6 cm) was only minimally less than typical scour depths in 2009 (~5 cm). Brown trout commonly exhibit lower egg burial depths than many other species (DeVries, 1997), particularly large, migratory species that may have scour depths up to 20 cm. Given these shallow burial depths, the increase in scour depth that might occur at larger floods exceeding bankfull could result in displacement of brown trout eggs.

Scour depth was strongly correlated with characteristics of the physical template occurring at a local scale and not a reach scale. Because brown trout preferentially selected sites of low shear stress (and therefore low scour depth) for spawning in our system, scour depths of brown trout spawning gravels did not increase with distance upstream despite an increase in reach shear stress. These results are in contrast to research conducted on the Trinity River, California, in which reach-scale shear stress and entrainment potential was positively correlated with reach-averaged scour depth (May et al., 2009). However, in that study, scour depth was measured across the entire reach and not just in spawning gravels, a difference which likely contributed to the apparent disparity between our results.

The positive, yet highly variable relationship we documented between local-scale estimates of shear stress and scour depth is similar to what has been observed in other systems (Rennie and Millar, 2000; May et al., 2009). At the same level of shear stress, some scour chains exhibited up to 4 cm of scour while others exhibited no scour. While higher estimates of shear

stress may represent a higher probability of scour, the occurrence and depth of scour cannot be precisely predicted due to its inherently stochastic and spatially variable nature (May et al., 2009). For instance, Rennie and Millar (2000) found no spatial auto-correlation in scour depths at closely spaced scour chains (~1 m), due to variable bed roughness and topography throughout the reach. Therefore, it is not surprising that we observed large variation in the relationship between local shear stress and scour depths. Further, even though the substrate size at spawning gravel patches was similar across reaches, the range of local shear stresses at which scour may occur is also dependent on sediment supply, the effects of bed structures and texture such as clusters and imbrication of particles, and shielding effects (Oldmeadow and Church, 2006; Shellberg et al., 2011).

We did not explicitly consider effects of sediment supply, armoring, bed structure and texture, and/or shielding in our evaluation of the relationship between our entrainment measures and scour depth, but anticipated that the relationship would differ between process zones due to differences in these factors. In contrast to the canyon and upstream zones, we observed that the dam backwater zone had comparatively higher scour depths for the levels of local shear stress and reach scale shear stress we observed. Whereas sediment-poor channels commonly exhibit partial mobility, sediment-rich channels can exhibit full mobility (Haschenburger and Wilcock, 2003). We hypothesize that abundant spawning gravel-sized substrate is supplied to the dam backwater reach from hillslopes immediately upstream. In addition, spawning throughout the channel each fall contributes to loosely-packed substrates and prevents extensive armoring. As a result, the critical threshold for particle mobility in the dam backwater channel may be lower than in the canyon and upstream zones. Therefore, the developing fry that remain in the gravel during the spring flood may be more susceptible to scour in the downstream, backwater reach than in upstream reaches.

Limitations and considerations

Our results support the idea that brown trout spawning gravels do not scour to depths necessary to harm developing fry during typical (i.e., at or near-bankfull) floods on the Logan River. While our sample sizes (n=18 in 2009 and n=32 in 2010) were considerably lower than some studies (Montgomery et al., 1996; Rennie and Millar, 2000; May et al., 2009), the patterns we observed are likely representative of scour depths that occur on the Logan River during typical flood years. We inserted a scour chain in major spawning patches in 2009 and in every spawning patch in the study reaches in 2010. Some variation likely occurred within each patch, but the consistently low scour depths and the significant relationship between local-scale estimates of shear stress and scour depth support our conclusion that scour depths were typically lower than burial depths of developing eggs and fry in 2009 and 2010. Nonetheless, several methods could be used to improve the accuracy of scour depth measurements. First, the use of sliding bead monitors would reduce the amount of error involved in measuring scour in the same locations between scour-and-fill events (Nawa and Frissell, 1993). Second, the ability to predict scour depths may be improved with more detailed estimates of water surface elevation, or estimates of local velocity above each scour chain.

Although our study did not officially extend into 2011, the flood in 2011 was one of the largest in recorded history for the Logan River. Of the scour chains that we were able to recover (~20%), those which exhibited minimal or no scour in 2009 and/or 2010 generally exhibited low scour depths and little fill in 2011. In contrast, at many locations exhibiting scour in 2009 and/or 2010 (including the Dewitt reach), extensive fill was deposited above the scour chains so that they could not be easily recovered in 2012. At several recovered scour chains, we observed both high amounts of fill and scour depths greatly exceeding average egg burial depths. These findings suggest that large floods, such as that occurring in 2011, may redistribute spawning gravels in this transport-limited system, causing deeper scour and mortality of early life-stages of

brown trout. Although further research is needed on how flood-related mortality during these large flood events could affect brown trout populations, we hypothesize that effects may be minimal due to the infrequency of these events.

While our results suggest that scour-related mortality of early life-stages may not be the primary mechanism influencing the upper distribution of brown trout on the Logan River, field surveys demonstrated a lower availability of spawning gravels at upstream, higher elevation reaches. We suggest that this lower gravel availability could limit spawning activity and establishment of brown trout in these reaches, which has been documented in other research (Beard and Carline, 1991). We are currently exploring this mechanism as part of other research efforts (e.g., Chapter 4).

CONCLUSIONS AND IMPLICATIONS

An understanding of the abiotic conditions that regulate brown trout populations is essential to predicting how climate change or habitat alterations may affect the distribution of brown trout. This knowledge may be especially important in systems where exotic brown trout co-occur with native trout species. In this study, we investigated trends in scour depths at brown trout spawning gravels along a longitudinal gradient of the Logan River, to determine whether higher scour depths could explain the low-densities of brown trout observed in upstream reaches. At floods near bankfull, scour depths of spawning gravels generally did not exceed egg burial depths. Across a longitudinal gradient, brown trout preferentially spawned in local areas with low shear stress, which contributed to the lack of a significant longitudinal trend in scour depths. Therefore, we conclude that spawning gravel scour is unlikely to be a dominant factor controlling the distribution of brown trout on the Logan River. Nevertheless, because brown trout at high elevations commonly emerge near the peak of the spring flood event, displacement of developing fry may contribute to low brown trout densities. Since actual displacement during flood events is

difficult to document, additional studies investigating the relationship between brown trout emergence timing and success of early life stages will be necessary to explore this mechanism. Warmer winters and large, earlier flood events (which are predicted to occur due to climate change) have the potential to affect brown trout populations by altering patterns of scour and/or emergence timing (Jonsson and Jonsson, 2009).

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CHAPTER 3

THE LONGITUDINAL DISTRIBUTION OF BROWN TROUT (*SALMO TRUTTA*) SPAWNING DENSITIES IN A MOUNTAIN RIVER: THE ROLE OF GRAVEL AVAILABILITY, PROPAGULE PRESSURE, AND OTHER HABITAT FACTORS

ABSTRACT

The distribution of brown trout in river networks may depend on the availability of suitable spawning gravels, but the influence of gravel availability versus other factors in determining brown trout distributions remains unexplored. To test our hypothesis that gravel availability is a primary factor controlling brown trout spawning densities along a longitudinal gradient of the Logan River, UT, we evaluated models which included estimates of gravel availability, as well as those containing predictors related to abiotic habitat conditions and propagule pressure (e.g., distance from source populations such as dam backwaters, tributaries, and beaver dams). We estimated gravel availability using both field and remotely-derived estimates of unit stream power and performed our analysis using a spatial hierarchical Bayesian modeling approach. Inclusion of spatial auto-correlation did not greatly improve the importance of the best model. Models which contained only estimates of unit stream power as a predictor exhibited low performance. However, models which contained other abiotic habitat and propagule pressure-related factors in combination with unit stream power exhibited high performance. Predictors included in many of the top models included those describing distance from dam backwaters, average temperature, and the extent of anchor ice cover. Redd densities, adult densities and top-predictors were highly correlated, suggesting that these factors may limit the adult distribution and invasion of high-elevation reaches by brown trout. Our results illustrate how estimates of unit stream power can be used to identify areas of gravel accumulation, but

suggest that the distribution of brown trout may be more limited by the location of source populations and availability of other suitable habitat conditions.

INTRODUCTION

The introduction of invasive species is one of the primary causes of biodiversity loss world-wide. As a result, understanding what factors influence the distribution of invasive species is a primary focus of ecological research. Species distribution models are empirical models that relate species' abundance or presence-absence data to characteristics of the abiotic environment. In invasive species research, such models can be used to quantify the environmental niche of an invasive species, test hypotheses regarding which abiotic factors most limit an invasive species, and assess the potential for spread of an invasive species due to climate or habitat alterations (Guisan and Thuiller, 2005)

More widely-available methods have increased the ease of incorporating and using spatially-explicit habitat data into models of invasive species distributions. For instance, recent advancements in remote sensing and Geographic Information Systems have allowed for the incorporation of remotely-estimated habitat characteristics and the analysis of invasive species-habitat relationships over large geographic areas (Rouget and Richardson, 2003; Joshi et al., 2006). Additionally, statistical methods that incorporate spatial auto-correlation have allowed for improvements in the predictive ability and interpretation of species distribution models (Guisan and Thuiller, 2005). Such tools could help inform our understanding of what abiotic environmental factors influence the invasion success of brown trout (*Salmo trutta*) within native stream communities.

Brown trout are among the world's top invasive species, displacing other fish species through both competition and predation (Lowe et al., 2000; McIntosh et al., 2011). In the Logan River, Utah, brown trout have largely displaced native Bonneville cutthroat trout (*Oncorhynchus*

clarki Utah), a species of concern, in downstream sections. Abundance of Bonneville cutthroat trout is still high in upstream, higher-elevation sections where brown trout are nearly absent (de la Hoz Franco and Budy, 2005; Budy et al., 2008). Such altitudinal species zonation has been observed in other stream systems containing both species, and a similar pattern occurs between brown trout and native brook trout in the eastern U. S. (e.g., Weigel and Sorenson 2001).

Past research has failed to identify the mechanism(s) responsible for these altitudinal zonation patterns. On the Logan River, this research has included studies focused on summer temperature effects on adult brown trout growth (de la Hoz Franco and Budy, 2005; McHugh and Budy, 2005), the outcome of competitive and temperature-mediated competitive interactions between brown trout and cutthroat trout (McHugh and Budy, 2005; McHugh and Budy, 2006), and effects of both winter temperature and scour on early-life stage survival of brown trout (Wood and Budy 2009, Chapter 2). While competition with brown trout limits cutthroat abundance in downstream reaches, these studies suggest that a yet unexplored abiotic mechanism or suite of mechanisms may be responsible for the near-absence of brown trout in upstream reaches.

A potentially important abiotic habitat factor affecting brown trout invasion success is the distribution of spawning gravels, which could result in low spawning densities and contribute to low adult abundance in upstream reaches. In comparison to other habitat factors, Beard and Carline (1991) demonstrated that spawning gravel availability was the most likely factor explaining the distribution of brown trout throughout a small drainage in Pennsylvania. Other research has documented the influence of the spatial arrangement of spawning gravels on trout meta-population dynamics (Petty et al., 2005; Hudy et al., 2010). More specifically, Petty et al. (2005) found that movement between spawning habitats in a West Virginia stream helped explain the abundance of brook trout (*Salvelinus fontinalis*) at a watershed scale, while Hudy et al. (2010) observed that the limited dispersal of brook trout from spawning areas helped account for within-

stream spatial population structure. Although some brown trout migrate to spawn, a large proportion choose spawning sites close (<300 m) to adult rearing habitat (Young et al., 1997; Bunnell et al., 1998; Burrell et al., 2000). As such, brown trout invasion potential and adult distributions could depend partly on dispersal from spatially-distributed spawning gravels. The absence of brown trout from higher-elevation portions of rivers could occur in different systems that similarly exhibit limited gravel availability due to low transport capacity (Montgomery and Buffington, 1997).

Geomorphic metrics can be used to predict areas of low transport capacity, and potential spawning gravel accumulation, within river systems. Buffington et al. (2004) predicted suitable spawning areas within a watershed network using estimates of median grain size (D_{50}), developed from remotely-derived slope and the shields equation. The Logan River is characterized by relatively coarse substrates, and spawning occurs at sizes much smaller than the D_{50} (Chapter 1). Nonetheless, textural complexity (or the number of patches with unique substrate sizes) generally increases as transport capacity decreases (Buffington and Montgomery, 1999). We hypothesize that unit stream power, a measure of transport capacity representing the potential rate of energy expenditure per unit weight of water, may be used to estimate potential areas of spawning gravel accumulation. In addition, all three of the parameters used to calculate unit stream power (slope, width, discharge) have been linked to distributions of brown trout (Bozek and Hubert, 1992; Rahel and Nibbelink, 1999). While these variables are indirect proxies for other factors actually driving abundance patterns, unit stream power integrates these metrics into single metric describing potential gravel accumulation.

Stream power metrics are frequently used to better understand geomorphic processes (Reinfelds et al., 2004; Jain et al., 2006; Jain et al., 2008), but the use of stream power to explain distributions of aquatic organisms has only recently being explored (O'Hare et al., 2011). Slope measurements, necessary components of power metrics, are commonly estimated using Digital

Elevation Models (DEMs) (Jain et al., 2006). Although DEM-based techniques provide an inexpensive way to estimate stream power metrics in a short amount of time, they can be both inaccurate and imprecise (Walker and Willgoose, 1999) which could mask relationships between unit stream power and species' distributions. Therefore, further research is needed on how closely remotely-derived unit stream power approximates field-derived unit stream power.

In addition, brown trout spawning densities on the Logan River may depend on other factors affecting spawners, early-life stages, and adults. Spawning densities are ultimately influenced by both spawning and adult habitat quality and abundance (Knapp et al., 1998; Palm et al., 2007). Propagule pressure, or the number of individuals introduced to an area, is also considered to be one of the most important factors influencing invasion success (Lockwood et al., 2005). Failure to consider these and other potentially influential factors could result in a misinterpretation of the relationship between gravel availability and spawning densities. Further, spatial auto-correlation is often observed in models when an important spatially-dependent habitat variable or ecological process was not included (Legendre and Fortin, 1989). Because of the assumption of independence in statistics, ignoring this spatial auto-correlation may lead to false conclusions about the importance of predictor variables in the model (Lichstein et al., 2002).

In this study, we used a Bayesian Conditional Auto Regressive (CAR) modeling framework to explore relationships between unit stream power versus other habitat variables in predicting the distribution of brown trout redd densities on the Logan River, Utah, USA. The specific goals of our research were to 1) examine the relationships among gravel availability, habitat and propagule pressure factors, and spawning and adult densities of brown trout and 2) develop a model to predict spawning densities from these factors, including field-derived unit stream power as an estimate of gravel availability. Lastly, we were also interested in whether a less precise, remote-estimate of unit stream power could be substituted for a field estimate, with similar results.

We hypothesized that unit stream power would be a significant predictor of availability of spawning gravels, due to the role of channel competence in determining substrate size (Buffington and Montgomery, 2004). Because of the importance of gravel-sized substrate for spawning (Miller et al., 2008), we also hypothesized that unit stream power would be among the top-predicting abiotic habitat variables in models to predict redd densities. Finally, we tested whether remote estimates of unit stream power would perform similarly to field estimates, due to potentially strong variation in slope along the longitudinal gradient of the Logan River. Such variation in slope, exhibited by this mountainous terrain, could outweigh variation caused by errors in the DEM.

METHODS

Study area description

This research was conducted on the Logan River, northern Utah, USA. The Logan River is a tributary of the Bear River, which terminates in the Great Salt Lake. The river is a snowmelt flood dominated system, and flood events typically occurring in May and June and decline throughout much of the summer. Three major tributaries flow into the Logan River within the study area, including Right Hand Fork, Temple Fork, and Beaver Creek (Figure 3.1).

A portion of the mainstem of the Logan River was selected for the study to represent the transition from high to low densities of brown trout that occurs longitudinally on the river. The study area extended from the impoundment of Third Dam to three km upstream of the confluence with Beaver Creek (Figure 3.1). Third Dam is the most upstream of a series of three dams on the river, and the impoundment upstream of Third Dam supports some of the highest densities of mature brown trout adults in the system (Saunders, personal communication). Few cutthroat trout occur downstream from Third Dam, and the hydrology downstream from the dam is highly altered by diversions. In contrast, Beaver Creek represents the upper extent of the brown trout

population, as no spawning or adult brown trout have been documented above the confluence with Beaver Creek. For a more detailed description of the study area, refer to Chapter 2.

Study design

During the years 2008-2010, we used a Topcon Hiper Pro GPS Unit (Topcon, USA) to perform longitudinal profile surveys of 75% of our 32 km study section of the Logan River. We collected elevation measurements at the bed and water surface, occurring at each break in

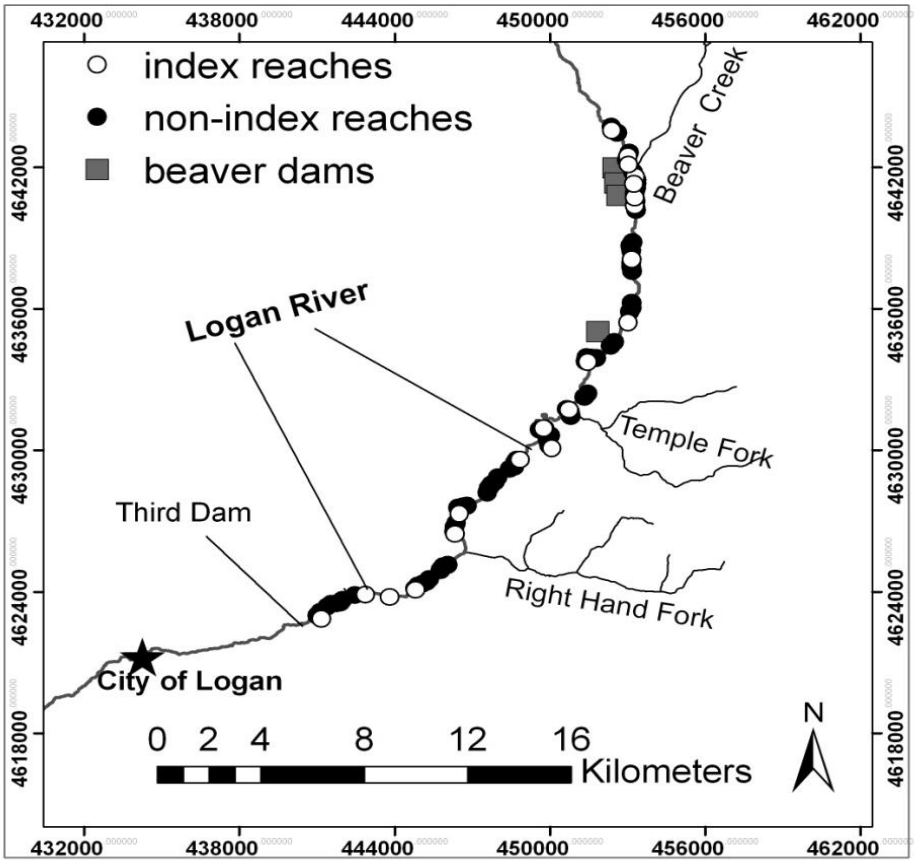

Figure 3.1. Study reaches and key features on the Logan River, Utah; index reaches are denoted by solid circles and non-index reaches are denoted by open circles. Key features include locations of beaver dams, Third Dam impoundment habitat, and spawning tributaries of Right Hand Fork and Temple Fork, as well as the tributary of Beaver Creek.

slope. The GPS unit was referenced to base station locations, and we mapped the locations of base stations using OPUS Positioning System, so that all surveyed points could be linked together using the UTM 12N- WGS84 coordinate system. We created line shapefiles of the completed sections of river in ArcMap 9.3, and all subsequent GIS analyses were performed using ArcMap 9.3. The horizontal accuracy of the satellite GPS unit is approximately 10 mm, while the vertical accuracy is 15 mm.

At a total of 83 reaches, each approximately 200 m in length, we measured predictors important to multiple life-stages of brown trout. These included unit stream power, as well as distance from potential source populations (i.e., propagule pressure), and physical habitat suitability. In addition, we quantified redd densities at each of the 83 reaches, which represented our index of brown trout invasion success.

In a subset of twenty reaches (hereafter referred to as "index" reaches), we collected more detailed data related to temperature predictors, gravel availability, as well as adult densities. We used data collected at index reaches to explore relationships between unit stream power and gravel availability, as well as redd and adult densities We also used data collected at index reaches to estimate values of temperature predictors at the remaining 63 reaches for use in models to predict redd densities. The twenty index reaches included eight long-term monitoring or previously-sampled reaches (Budy et al., 2008; Wood and Budy, 2009) and thirteen additional randomly-selected reaches.

Predictor variables

We measured a suite of habitat factors potentially influencing brown trout redd and/or adult densities. We hypothesized that some of these factors directly influence redd densities, including those related to gravel availability (unit stream power) and egg and fry survival (e.g., winter water temperatures and presence of anchor ice). We also included factors which we

considered to indirectly affect redd densities through their influence on adult densities, including factors related to physical habitat suitability (velocity and depth) and growth and physiological requirements (average annual and maximum water temperatures). Finally, we estimated the influence of propagule pressure (or the number of individuals introduced to the study area) on brown trout spawning densities. Propagule pressure is a major determinant of which habitats are successfully established by invaders (Havel and Shurin, 2004). For our study, we assumed that propagule pressure could be represented by the distance from source areas previously identified to contain high densities of brown trout due to potential past stocking and/or ideal habitat conditions.

For each of the 83 study reaches, we estimated field-derived unit stream power (ω) as an index of transport capacity and spawning gravel availability ("pwr"). We calculated unit stream power ($Ns^{-1}m^{-1}$) as follows:

$$\omega = \frac{\gamma * Q * s}{w}$$

where γ is the unit weight of water (9800 N/m^3), Q is discharge (m^3), s is slope (m), and w is bankfull width in meters (Jain et al., 2006). We calculated slope of each reach as follows:

$$\frac{Max - Min}{Length}$$

where *Max* is the elevation at the top of the reach, *Min* is the elevation at the bottom of the reach, and *Length* is the length of the reach estimated by connecting field GPS locations.

We estimated bankfull discharge (Q) from stage height-contributing area relationships developed from three pressure transducers located in the study portion of the Logan River (Majerova and Schmidt, 2009-2010). For our purposes, we considered the peak discharge that occurred in 2009 to represent bankfull discharge, because the flow at long-term study reaches on the Logan River just exceeded the banks. We based bankfull width on field measurements of

wetted width performed in study reaches in 2010, and a relationship between wetted width and bankfull width developed for the Logan River.

In order to test our hypothesis that unit stream power can be used to estimate spawning gravel availability, we developed indices of spawning gravel availability for the twenty index reaches and compared trends in these measures to our unit stream power measures. To develop an index of proportion of substrate particles in the spawning gravel range, we divided each reach into unique morphological units (run, riffle, pool, cascade), and performed 100-point counts of bed material in each unit (Wolman, 1954). We quantified the number of particles between the sizes of 5.7 and 45 mm for each unit, and estimated the proportion gravel for each reach based on the percent of the reach comprised of each unit (Kondolf, 1997). Because smaller values are generally underestimated in pebble counts, we used a lower value of 5.7 mm, which is within the range of "fine gravel" (Kondolf, 1997). We used an upper value of 45 mm, because previous surveys of redds showed that substrates chosen for spawning on the Logan River were consistently 45 mm or less in size (Chapter 2). To develop a second index of spawning gravel availability, we visually documented the location and size of spatially contiguous portions of the reach (e.g. "patches") containing both positive velocities and dominated by substrate within the spawning gravel range (5.7 and 45 mm), which we considered to be preferred for spawning by brown trout based on previous redd surveys. We divided the proportion of the reach covered by these spawning gravel patches by the total area of the reach (average width X length) to obtain an estimate of "proportion covered in spawning gravel patches". We used linear regression to investigate the relationship between unit stream power and proportion spawning gravel and unit stream power and proportion of reach covered by spawning gravel patches.

We calculated remotely-derived unit stream power ("gispwr") GIS methods (slope and discharge) and hydraulic geometry relationships (width). We estimated the 2-year recurrence discharge at each index reach using Utah Stream Stats

(http://water.usgs.gov/osw/streamstats/utah.html), and scaled it to the 2-year recurrence interval at the Logan River USGS gage. We used this relationship to predict bankfull discharge at each study reach. We determined slope from 10-meter DEMs according to the profile-smoothing technique of Jain et al. (2006). We obtained 10-meter DEMs from the Utah GIS Portal (http://gis.utah.gov), where the 10-meter DEM was created by the United States Geological Survey (USGS) from hypsographic and hydrographic vector maps. We used hydrology tools in Arcmap to generate the Logan River streamline from flowpaths and calculated slopes based on measurements taken at the midpoint of each reach. Finally, we determined bankfull width from hydraulic geometry relationships developed between contributing area and bankfull width, developed for the Bear River Basin. We compared field-estimated slope to remotely-derived slope using linear regression.

We derived a predictor variable describing average winter temperature in each of our study reaches. Even though previous research on the Logan River has shown relatively low mortality of overwintering eggs and fry (Wood and Budy, 2009), other research suggests negative effects of winter water temperatures on early-life stages can occur as a result of low dissolved oxygen concentrations and freezing (Stonecypher et al., 1994). We used a combination of HOBO and Maximum i-button temperature loggers to estimate average winter temperature ("mntmp") at each of our twenty index reaches during the early-life stage incubation period (10 Nov 10 to 30 April), and a smoothing spline regression in R to predict values at non-index reaches. We used daily average water temperatures, which we averaged across the time period, in all calculations. We adjusted this and all subsequent temperature measurements to reflect the resolution of the i-button loggers, as the HOBO loggers and the i-buttons had resolutions of 0.10 ° C and 0.50 ° C, respectively.

We also included a variable describing the extent of anchor ice cover. We observed that anchor ice formed in low-temperature reaches as early as November, preventing access to

spawning gravels and upstream movement. We documented that anchor ice formed when water temperatures were at or below 0.50 ° C; therefore, we estimated the prevalence of anchor ice as the number of days when water temperatures were ≤ 0.5 ° C during the spawning season (10 Nov 2010 to 31 Nov 2010, "bel"). As with estimates of winter temperature, we collected temperature data at index reaches and used smoothing spline regression in R to predict number of days below zero at non-index reaches. Finally, we determined the potential barrier that anchor ice posed to upstream movement ("dist0"). We estimated the "dist0" variable by determining the cumulative number of days where the temperature ≤ 0.5 ° C and below, measured in an upstream direction from the high-density Third Dam impoundment area.

At all 83 reaches, we used reach average baseflow depth (m) and reach average baseflow velocity (m/s) as estimates of physical habitat suitability for spawning and adult brown trout. Even though more local estimates of habitat suitability would have been preferred, previous research has shown that easily obtained reach-level estimates can also explain abundance patterns (Ayllon et al., 2010). We estimated baseflow depth ("dpth") at the centerline of each reach from longitudinal survey data. We recognized baseflow estimates to be appropriate, because near-baseflow conditions are present during much of the year, and spawning occurs at near-baseflow conditions. In addition, depth could easily be taken from previously collected longitudinal profile data. Average baseflow water depth at each point in the long-profile was estimated by subtracting the bed elevation from the water surface elevation. We calculated mean reach depth by averaging depth measurements across the reach and average velocity ("vel") of each reach by dividing an estimate of the baseflow discharge at each reach by an estimate of cross-sectional area (reach average width * reach-average depth), where baseflow discharge in m^3 was estimated at each reach using a baseflow discharge-contributing area relationship developed from pressure transducers at key locations on the Logan River.

We generated variables describing both summer and average water temperatures of each reach. While neither summer or average water temperatures have been firmly established as dominant factors affecting the brown trout distribution in this system (McHugh and Budy, 2005), temperature effects cannot be ruled out due to their potential effects on growth and survival of brown trout in this and other systems (Elliott, 1976; Budy et al., 2008). Therefore, we included both summer ("mxtmp") and average water temperatures ("avtmp") as predictor variables. We employed methods similar to those used for estimating average winter temperature, except that we calculated average water temperatures over the entire study period (10 Nov 2009 to 9 Nov 2010) and summer water temperatures from 1 July 2010 to 31 Aug 2010.

We estimated variables describing the potential amount of propagule pressure. Anecdotal evidence suggests that the Third Dam impoundment was a brown trout stocking area (Figure 3.1), and the impoundment supports some of the highest densities of brown trout on the river. Therefore, we included distance to Third Dam ("dist") as a predictor affecting redd densities. We calculated distance (m) using the Flow Length tool in Arcmap and a stream layer digitized from the longitudinal profile and aerial photos of the Logan River.

We also included a propagule pressure predictor variable describing the distance (m) from each study reach on the mainstem to other non-mainstem habitats that could positively influence mainstem densities (i.e., source areas; "src"). In addition to being a potential introduction area, the impoundment of Third Dam supports extremely high density of reproductively mature brown trout (same comment as above). Therefore, we considered distance to the impoundment to be a source area. We also considered the high-density spawning tributaries of Right Hand Fork and Temple Fork to be source areas. Finally, we considered large beaver dams located adjacent to the river mainstem to be source areas. Other research has shown that beaver ponds may provide important overwintering habitat for salmonids (Cunjak, 1996), and we similarly observed large brown trout overwintering in these beaver ponds. We combined

"distance to high-density tributaries," "distance to beaver dams," and "distance to third dam" into one "distance to source" variable describing the distance to the nearest of these three sources. We weighed all sources similarly in our calculation, because we did not have any quantitative way to evaluate the relative contribution of each source to brown trout densities.

Redd densities

We counted redds (redd) in the Logan River during the fall spawning season during the years 2008-2011. We performed at least two years of redd surveys in each study reach. Samplers walked upstream, recording the presence of a redd feature (disturbed gravel with a pit and tailspill). The redd was given a score based on the likelihood that the feature was truly a redd, with the following scoring system: 1, extremely defined redd with spawning pair of brown trout; 2, extremely defined redd with no spawning pair; and 3, poorly defined redd with no spawning pair. We calculated the number of redds in each reach as the average number of redds in that reach during the years that it was surveyed, including only those redds with a score of "1" or "2". We calculated redd density as the number of redds/m^2, using the length and average wetted width of the reach to estimate area. For statistical purposes, we scaled the redd density in each reach to a count representing the number of redds/2000 m^2, a typical reach area.

Adult densities

We used snorkeling to quantify the abundance of brown trout in the twenty index reaches, for comparison with redd densities and abiotic variables. Surveys consisted of two snorkelers swimming adjacent to each other in the upstream direction, from the bottom to top of the reach. Each snorkeler marked the number of each species of fish observed, communication with his/her partner to make sure fish were not double-counted. We calculated an in index of brown trout adult density in each reach as the number of brown trout observed/m^2.

Statistical analysis

We evaluated the strength of relationships between abiotic variables and redd densities at all 83 reaches, and abiotic variables and adult densities at the twenty index reaches (where adult data was collected) using Pearson's correlation. We performed this and all other statistical analyses using the Program R (R Core Development Team, 2011).

We used a Bayesian Conditional Autoregressive (CAR) modeling approach to explore the most important abiotic habitat variables for predicting brown trout redd densities on the Logan River. We developed all models using the integrated nested Laplace approximations (INLA) package (Rue et al., 2009; R Core Development Team, 2011). The INLA method uses a deterministic approach to Markov Chain Monte Carlo (MCMC) simulation which computes direct approximations to posterior marginal distributions (Rue et al., 2009). The benefit of using INLA in comparison to a non-Bayesian approach is the ability to utilize a non-gaussian likelihood estimator and to include areal spatial processes. Non-gaussian likelihood estimators such as the zero-inflated, negative binomial likelihood used here can provide a better fit to over-dispersed data (i.e., the variance is high compared to the mean).

We implemented the hierarchical model as follows:

1) $y_i \sim \begin{cases} NegBinom\left(\mu_i, \varphi\right) & , with\ probability \quad p \\ 0\,, & , with\ probability \quad 1-p \end{cases}$

   i=1,…,n

2) $log(\mu_i) = \beta_0 + \beta_1 X_{i+\cdots\cdots} \beta_q X_{qi} + \varepsilon_i$, where $\varepsilon \sim N(0, \Sigma)$

3) $\beta_o, \beta_j \sim$N(0,1000), where j=1,…q

4) $(\sigma^2)^{-1} \sim$Gamma (1, 1/20000)

5) $\varphi \sim N(0{,}100)$, $logit\ (p) \sim N(-1{,}0.2)$

where equation 1 describes the negative binomial likelihood, with μequal to the negative binomial mean, φ representing the overdispersion portion of the negative binomial likelihood, and p equal to the zero inflation probability; equation 2 is the process model, with model covariates $\beta_{q\ldots qi}$ and error, ε_i, drawn from the covariance matrix Σ; and equations 3-5 are the priors of the gamma distribution for the spatial areal process. Non-informative priors were used for all fixed variables. We chose default hyperpriors for the precision (a=1) and smoothing (b=0.001) component of the spatial random effect. The areal process was omitted from non-spatial models.

We used a combination of Deviance Information Criteria (DIC) and a leave-one-out cross validation measure as described in (Schrödle et al., 2010) to evaluate competing models:

$$lnCPO = -mean(\log(CPO))$$

where CPO is the cross-validated predictive probability mass at each observation (CPO), and DIC is calculated automatically by the INLA program. Smaller values of DIC and CPO indicated better fit. We also computed the r^2 between observed and predicted values for each model, which we refer to as a "pseudo r-square" (given that our models are not linear) as another way of assessing each model's predictive power. In order to compare models, we performed computation of delta DIC using methods described in Burnham and Anderson (2002). We used untransformed predictor variables in all models, as equal variance is not an assumption of generalized linear models (Bolker et al., 2009). We did not evaluate candidate models if the model fit was not improved due to the presence of high collinearity ($r > 0.40$) between predictors.

RESULTS

Longitudinal surveys demonstrated that study reaches span a wide range of stream gradients. The lowest-gradient part of the study area, with a gradient of ~ 0.003, is the reach

immediately upstream of the Third Dam impoundment. Elsewhere, gradients range between 0.007 and 0.023 downstream of Temple Fork confluence and between 0.017 and 0.028 upstream from Temple Fork confluence.

Gravel accumulates in reaches with lower unit stream power. At our reaches, unit stream power significantly predicted proportion gravel at the 20 index reaches ($F_{1,18}$=7.34, p=0.014,R^2=0.250, Figure 3.2 A.). The amount of variance explained increased ($F_{1,17}$=13.19, p=0.002,R^2=0.413) with the removal of an outlier (outlier: gravel availability =0.09; Figure3.2 A). Unit stream power was also a significant predictor of the proportion comprised of gravel patches, exhibiting a negative exponential relationship to this response variable (R^2=0.937, p <0.0001; Figure 3.2 A.)

Both measures of gravel availability significantly predicted redd densities at index reaches. The proportion gravel exhibited a positive, exponential relationship to redd densities (p<0.001, R^2=0.662; Figure 3.2 B). The proportion comprised of gravel patches exhibited a positive, linear relationship to redd densities ($F_{1,17}$=159.49, p<0.0001,R^2=0.893; Figure 3.2 B).

Across our 83 reaches, remotely-derived stream power closely approximated field unit stream power, which we recognized as being closer to the "truth." We observed a significant, positive correlation between these two measures (r=0.392, p< 0.0002, DF=81). However, remotely-estimated unit stream power exhibited strong variance between reaches in close proximity, while field unit stream power exhibited more gradual changes (Figure 3.3) along a longitudinal gradient. Our remote estimates of slope, a key component of the unit stream power estimate, significantly predicted field slope (R^2=0.446, p<0.0001, DF=80). However, remote estimates over-predicted at low slopes and under-predicted at high slopes (Figure 3.4, RMSE=0.006).

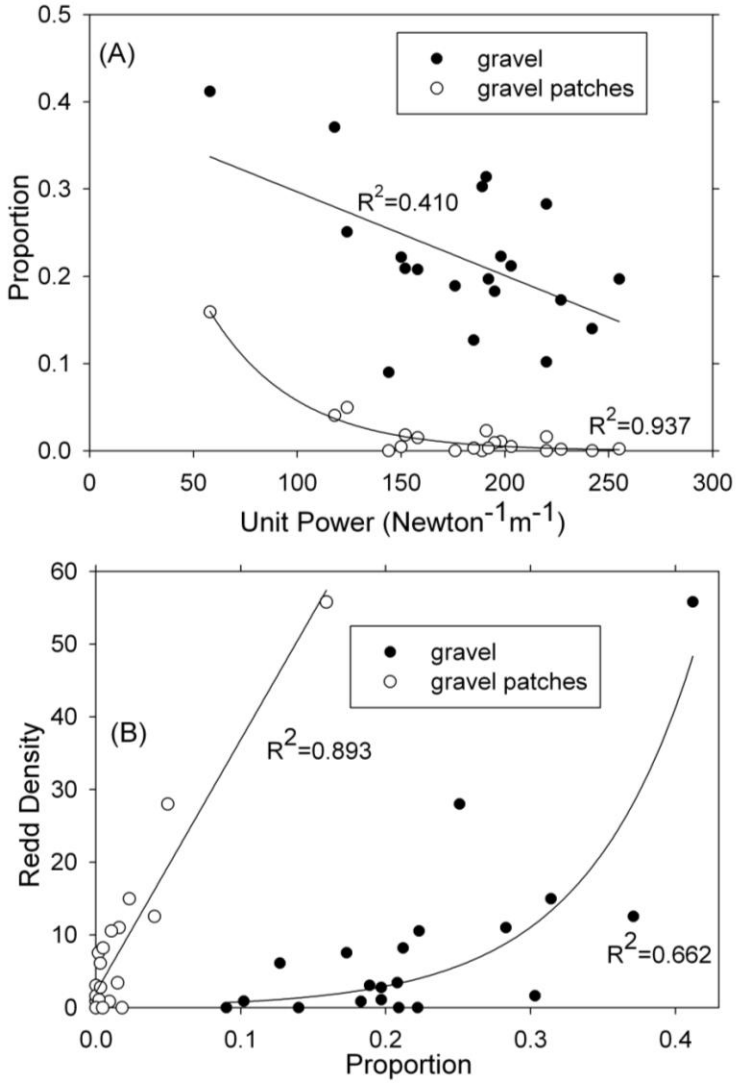

Figure 3.2 A,B. Scatterplots showing A) the negative relationship between unit power and proportion gravel, and between unit power and proportion comprised of gravel patches B) The positive relationship between proportion gravel and redd densities, and between proportion comprised of gravel patches and redd densities.

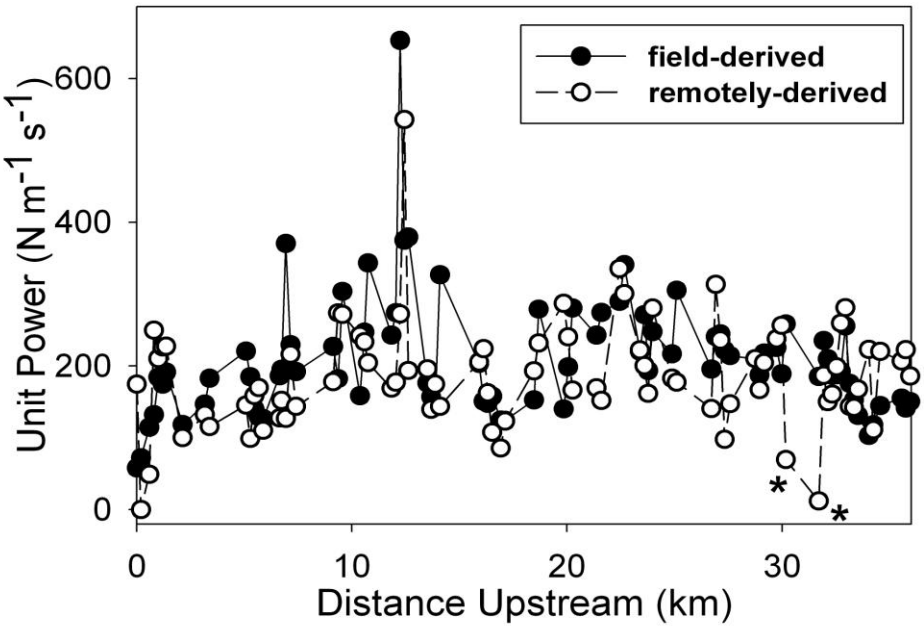

Figure 3.3. A comparison of change in field-derived and remotely-derived unit stream power with distance upstream (n=83).

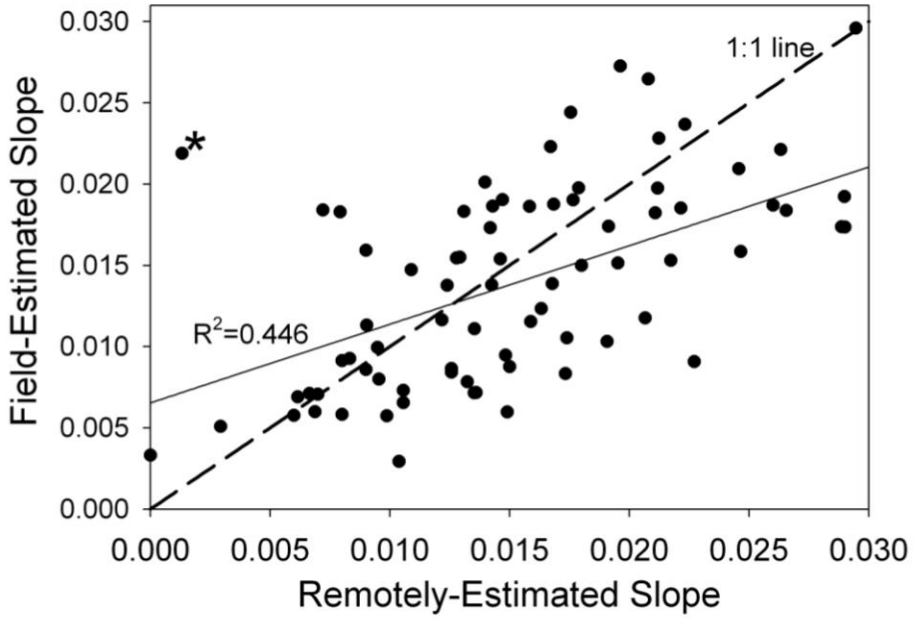

Figure 3.4. Scatterplot illustrating the relationship between field-estimated slope and GIS-estimated slope (R^2=0.446, n=82, after removal of outlier-*). Deviations from the 1:1 line (dashed) indicate over-estimation at low slopes and under-estimation at high slopes, compared to field measures.

Downstream reaches generally exhibited higher summer and winter water temperatures than upstream water temperatures (Figures 3.5A, C), and average water temperatures declined linearly from downstream to upstream (Figure 3.5A). We observed the highest summer water temperatures (Figure 3.5B) and lowest winter water temperatures (Figure 3.5C) in a middle portion of the river. This middle section of river, where we also observed the greatest anchor ice presence, experienced the greatest number of days ≤ 0.5 °C (Figure 3.5D).

We observed strong correlations among many of our predictor variables, especially those related to temperature (Table 3.1). For instance, we documented strong correlations between average and maximum temperature (r=0.68), minimum temperature and number of days below

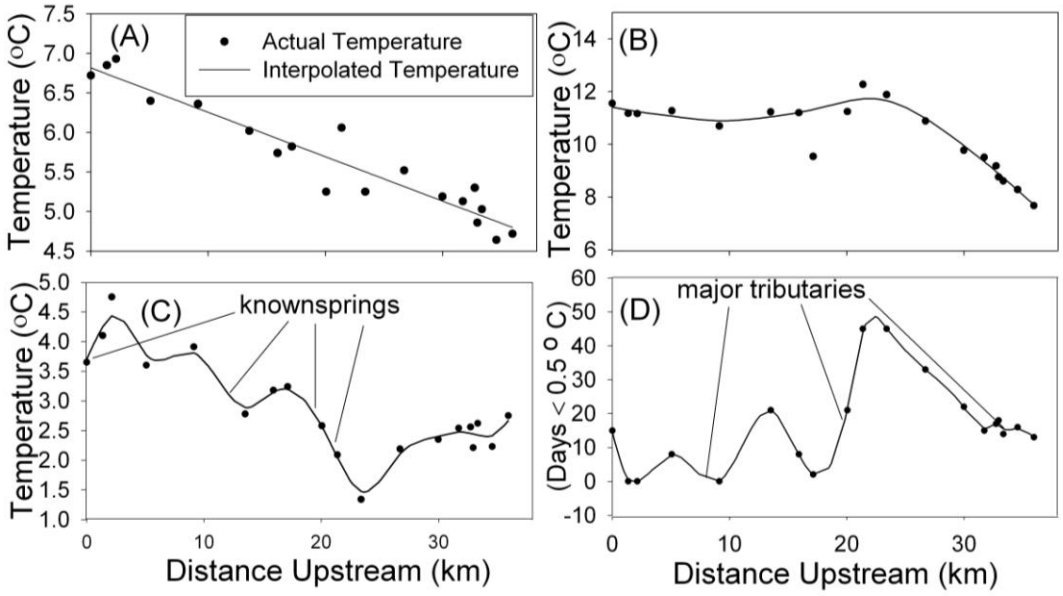

Figure 3.5,A-D. Actual versus interpolated water temperature measures versus distance upstream, including A) average temperature, B) summer water temperature, C) winter water temperature and D) number of days ≤ 0.5 °C as an index of the presence of anchor ice. Locations of known springs are estimated based on Spangler 2001.

1°C (r=-0.88), and average depth and average temperature (r=-0.74). Distance from Third Dam also demonstrated a strong, positive correlation with each of the three temperature variables (maximum, minimum, and average temperature). Distance from Third Dam was directly correlated with average temperature, as a result of the use of distance to predict average temperature at non-index sites (Figure 3.5A) .

Our results demonstrated a strong correlation between redd and adult densities at our twenty index reaches (r=0.86; Table 3.1). In terms of abiotic predictors, brown trout adult densities were most strongly correlated with average temperature and distance from Third Dam (r = 0.82 and r =-0.82, respectively) , as well as minimum temperature (r=0.71) and our anchor ice barrier predictor (r=-0.70). Redd densities were also most highly correlated with average temperature/distance from Third Dam (r=0.54 and r=-0.54, respectively), minimum temperature (r=0.47) and our anchor ice barrier predictor (r=-0.45).

The performance of the best-performing non-spatial models was unaffected when we included spatial structure. In contrast, the performance of many previously low-performing models improved when spatial structure was added. Inspection of covariate means suggested spatial confounding, or the presence of strong correlations between spatial structure and model covariates (Hodges et al., 2010). This spatial confounding may have affected the relative performance of covariates in our spatial models. Therefore, we defaulted to the outcome of our non-spatial models to evaluate the most important abiotic habitat factors influencing spawning densities.

Our top-performing non-spatial models included predictors describing distance from Third Dam impoundment (an index of propagule pressure) or average temperature, and either field or remotely-derived unit stream power (Table 3.2). Our estimates of average temperature and distance from Third Dam could be used interchangeably in models with essentially no effect on model fit, because of the direct correlation between these two variables. Remote stream power

generally exhibited similar performance as field stream power, but this varied by model. The best overall model described an interaction between our anchor ice barrier predictor and our field measure of unit stream power (Figure 3.6). Some of the poorest performing models included physical parameters of velocity and depth, and temperature variables with the notable exception of average temperature.

DISCUSSION

The distribution of brown trout in river systems likely depends on a range factors important to early-life stages, spawners, and adult brown trout. Herein, we tested the hypothesis that gravel availability significantly influences redd densities and overall brown trout invasion success on the Logan River, Utah. To do this, we investigated how a suite of predictors influenced redd densities, including variables describing abiotic variables such as gravel availability and physical habitat suitability as well as propagule pressure (Elliott, 1976; Stonecypher et al., 1994; Lockwood et al., 2005; McHugh and Budy, 2005).

As we hypothesized, unit stream power was a significant predictor of gravel availability. Yet the relationship between unit stream power and overall proportion gravel was relatively weak. Gravel availability is influenced by inputs from tributaries and hillslopes, as well as variability in substrate roughness, which were not incorporated into our analysis and may have affected the strength of the relationship between unit power and gravel availability (Miller et al., 2008). The proportion comprised of spawning gravel patches was a stronger predictor of redd densities compared to the proportion of particles that were of spawning gravel size, demonstrating that the spatial arrangement of spawning gravels may be more important than the absolute number of spawning gravels.

Strong correlations among our predictor variables suggested that many factors besides gravel availability interacted to affect redd and brown trout densities. While some factors

Table 3.1. Matrix showing Pearson's correlation between adult densities, redd densities, and predictors at the twenty index reaches, and redd densities and predictors at all 83 reaches. Adlt =adult densities; redd=redd densities; dist=distance from Third Dam; src=source areas; avtmp=average temperature; maxtmp= maximum temperature; mntmp=minimum temperature; bel=number of days ≤ 0.5 °C; dist0=cumulative anchor ice days; pwr=field unit power; gispwr=remote unit power; dpth=reach-average depth; vel=reach-average velocity.

	abundance estimates		intro/source areas		growth/ physiology		winter survival			gravel		physical habitat	
	adlt*	redd	dist	src	avtmp	mxtmp	mntmp	bel	dist0	pwr	gispwr	dpth	vel
redd	0.86	1.00	-0.54	-0.10	0.54	0.31	0.47	0.30	0.45	0.35	-0.34	0.34	-0.14
dist	-0.82	-0.54	1.00	-0.14	-1.00	-0.68	-0.82	0.51	0.96	0.02	0.12	-0.74	0.15
src	-0.61	-0.10	-0.14	1.00	0.14	0.12	0.14	0.08	0.20	0.16	0.02	0.14	0.14
avtmp	0.82	0.54	-1.00	0.14	1.00	0.68	0.82	0.51	0.96	0.02	-0.12	0.74	-0.15
mxtmp	0.51	0.31	-0.68	0.12	0.68	1.00	0.21	0.12	0.78	0.21	0.03	0.44	0.31
mntmp	0.71	0.47	-0.82	0.14	0.82	0.21	1.00	0.88	0.72	0.21	-0.21	0.65	-0.42
bel	-0.41	-0.30	0.51	-0.08	-0.51	0.12	-0.88	1.00	0.42	0.30	0.21	-0.46	0.51
dist0	-0.70	-0.45	0.96	-0.20	-0.96	-0.78	-0.72	0.42	1.00	0.09	0.04	-0.71	0.06
pwr	-0.41	-0.35	0.02	0.16	-0.02	0.21	-0.21	0.30	0.09	1.00	0.39	0.11	0.26
gispwr	-0.08	-0.34	0.12	0.02	-0.12	0.03	-0.21	0.21	0.04	0.39	1.00	-0.02	0.08
dpth	0.64	0.34	-0.74	0.14	0.74	0.44	0.65	0.46	0.71	0.11	-0.02	1.00	-0.49
vel	-0.10	-0.14	0.15	0.14	-0.15	0.31	-0.42	0.51	0.06	0.26	0.08	-0.49	1.00

Table 3.2. Results of A) non-spatial and B) spatial models, testing the influence of potential abiotic variables on redd densities. △DIC and △CPO was calculated relative to the best model (denoted with an (*)).

	(A) non-spatial					(B) spatial			
	DIC	△DIC	△CPO	r^2		DIC	△DIC	△CPO	r^2
pwr*dist0	393.71	0.05	2.37	0.69	pwr*dist0 (*)	393.66	0.00	2.37	0.69
gispwr + dist	401.73	8.07	2.42	0.51	gispwr	394.14	0.48	2.38	0.63
avgtmp + gispwr	401.73	8.07	2.42	0.51	src + gispwr	394.36	0.70	2.40	0.63
gispwr* dist0	402.02	8.36	2.42	0.45	gispwr + dist	400.23	6.57	2.40	0.55
pwr * dist	402.19	8.53	2.42	0.72	vel	397.62	3.96	2.41	0.71
pwr * avtmp	402.22	8.56	2.42	0.72	avtmp + gispwr	400.22	6.56	2.41	0.55
pwr + dist	406.49	12.83	2.45	0.56	src	397.28	3.62	2.42	0.76
avtmp + pwr	406.49	12.83	2.45	0.56	bel1	398.25	4.59	2.42	0.67
dist	408.83	15.17	2.46	0.41	mxtemp	398.44	4.78	2.42	0.71
avgtmp	408.83	15.17	2.46	0.41	pwr	399.44	5.78	2.42	0.73
avtmp + bel0	410.00	16.34	2.47	0.37	gispwr * dist0	401.96	8.30	2.42	0.45
avgtmp + src	410.98	17.32	2.48	0.41	pwr * dist	402.02	8.36	2.42	0.72
dist0	412.46	18.80	2.49	0.26	avtmp * dist	402.02	8.36	2.42	0.72
mxtmp	418.15	24.49	2.52	0.15	src + pwr	400.37	6.71	2.43	0.75
mntmp	421.42	27.76	2.54	0.18	avtmp + bel0	401.35	7.69	2.43	0.61
dpth	434.74	41.08	2.62	0.02	avgtmp	403.01	9.35	2.43	0.61
pwr	436.28	42.62	2.63	0.28	dist	403.16	9.50	2.43	0.61
bel1	436.32	42.66	2.63	0.08	dist0	402.96	9.30	2.44	0.68
gispwr	437.50	43.84	2.64	0.18	avgtmp + src	402.99	9.33	2.44	0.68
src + pwr	438.04	44.38	2.64	0.23	avtmp + pwr	406.20	12.54	2.45	0.57
src + gispwr	438.45	44.79	2.64	0.19	pwr + dist	406.20	12.54	2.45	0.57
vel	447.23	53.57	2.70	0.00	depth	399.33	5.67	2.47	0.73
src	448.45	54.79	2.70	0.00	mntmp	399.35	5.69	2.47	0.73

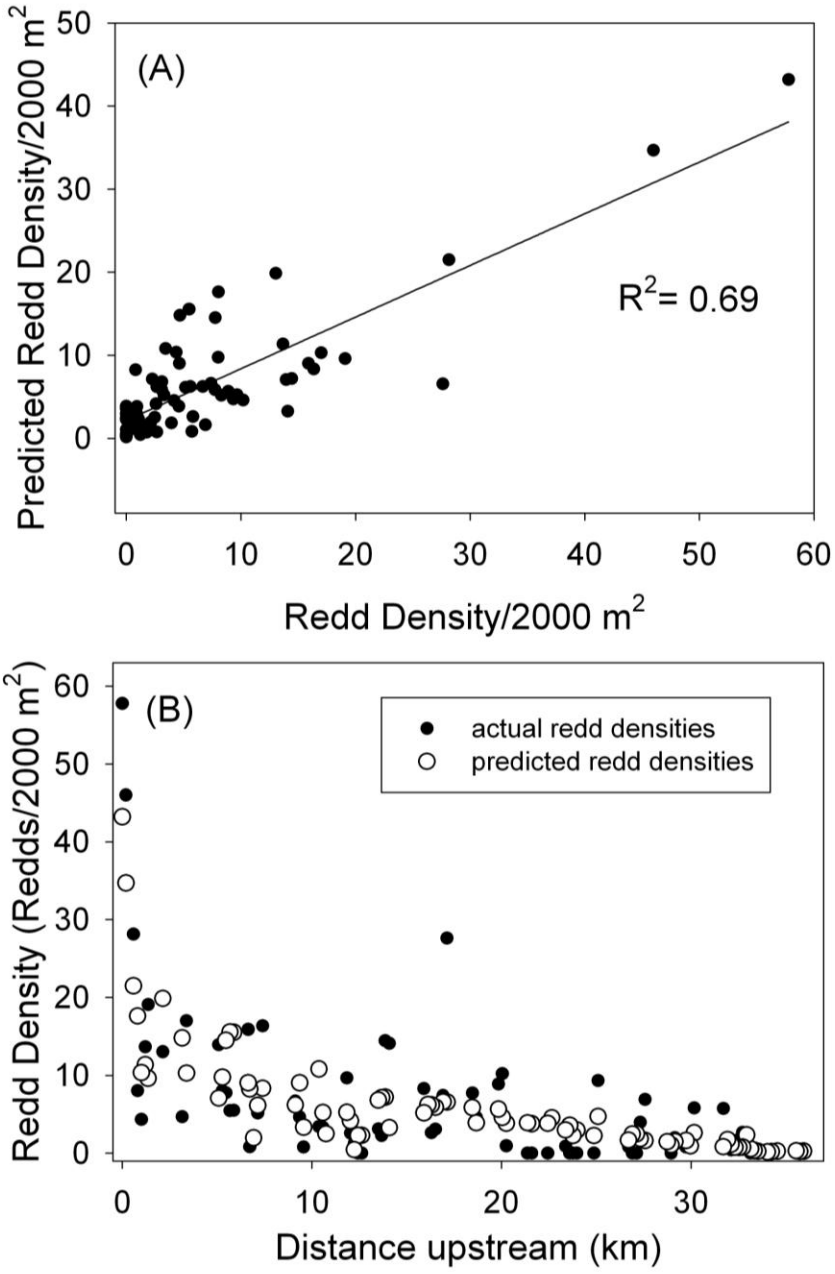

Figure 3.6 A,B. Relationship between and actual redd densities, including A) A scatterplot demonstrating the strong correlation between actual and predicted redd densities and B) A plot of actual versus predicted redd densities along the longitudinal gradient

may directly affect spawning habitat, the density of redds is also determined by the number of mature, adult trout present (Beard and Carline, 1991; Al-Chokhachy et al., 2005). As a result, it may be difficult to discern whether abiotic factors influence the distribution and density of redds directly or indirectly through their effect on adults. In our study, the same habitat variables were strongly correlated to both redd and adult densities: average temperature and/or distance from Third Dam, anchor ice as a barrier to movement upstream, and minimum temperature. Therefore, these abiotic factors may contribute to brown trout invasion success and abundance of both early and adult life-stages on the Logan River. Other research suggests that the most successful invaders are those which can exploit habitat at multiple life stages (Kolar and Lodge, 2002), and such an ability may contribute to brown trout invasion success worldwide.

We observed that the performance of individual models varied depending on the measure used (e.g., DIC, CPO, or pseudo r^2). Specifically, results for DIC, CPO, and pseudo-r^2 differed across models. Because of the large number of parameters in our models, it is not surprising that the results were not consistent across measures. The pseudo-r^2 does not account for the number of parameters in the model and is considered a biased measure of performance. While the CP0 (a leave-one-out cross-validation measure) is less biased, it also does not control for the number of parameters. Because our main goal was to evaluate model performance and not necessarily to predict redd densities accurately, we used DIC to evaluate model performance.

We used our non-spatial models in order to evaluate the influence of unit stream power and our other potential predictor variables on redd densities, in order to avoid the effects of spatial confounding in our spatial models. While spatial confounding probably occurs frequently in spatial models, its effect on model outcomes is only currently being recognized in the literature (Paciorek, 2009; Hodges et al., 2010). Such spatial confounding occurs when two non-spatial covariates are highly correlated and one of the covariates is reduced to a near-zero coefficient. In our spatial models, the coefficient of the non-spatial covariate was reduced to being close to zero.

In spatial models, few approaches exist to address high correlation between unexplained spatial variation and non-spatial covariates (Hodges et al., 2010). Failing to account for spatial auto-correlated error can result in ascribing significance to the wrong predictors; however, in this case accounting for spatial auto-correlation actually reduced our ability to interpret the best predictors. In addition, because some of the top non-spatial models exhibited high levels of performance, we used the outcome of our non-spatial models to evaluate top predictors.

Contrary to our hypothesis, model outcomes demonstrated that unit stream power alone was not a good predictor of redd densities. Based on our field observations, limited spawning occurred in some reaches with adequate spawning gravels, suggesting that other factors were more limiting. Even so, our results indicated that much of the spatial variation in redd densities could be accounted for by our top-performing abiotic predictor variables in conjunction with unit stream power. For instance, although redd densities showed a general decrease with distance from Third Dam, local areas of high redd density occurred in portions of the river with low unit stream power. Therefore, gravel availability likely contributed to some of the spatial structure in redd densities, although not necessarily to the decrease in redd densities with distance upstream.

In contrast to unit stream power, average temperature (avtmp) and distance from Third Dam impoundment (dist) alone were good predictors of redd densities. These could be used interchangeably with no effect on performance in our models, limiting our evaluation of which factor has greater or lesser influence on redd densities. In other research, both the importance of propagule pressure and temperature demonstrated a significant relationship to brown trout distributions (Bozek and Hubert, 1992; Westley and Fleming, 2011). On the Logan River, upstream reaches exhibit water temperatures which are generally lower than what is optimal for brown trout growth (Budy et al., 2008). Yet, experimental manipulations have demonstrated that brown trout growth at these high elevations actually exceeds cutthroat trout growth. Therefore, while average temperature may have some effect on the brown trout distribution, we hypothesize

that distance from Third Dam is a more dominant factor influencing the establishment and invasion success of brown trout in upstream reaches. The Logan River upstream of Third Dam represents an area of high propagule pressure, due to potential past stocking, abundant spawning gravels, ideal water temperatures, and proximity to impoundments containing high densities of brown trout. Some of the highest brown trout densities in the study area occur in the portion of river immediately upstream of the impoundment (Saunders, personal communication), illustrating the importance of Third Dam as a source area for brown trout.

Despite the high-performance of the Third Dam predictor variable, the best overall model included an interaction between anchor ice as a barrier (dist0) and field unit power (pwr). The "dist0" predictor is essentially a modified version of the "dist" variable that incorporates the potential for anchor ice to act as a barrier to upstream movement. This model outperformed nearly all of our spatial as well as most of our non-spatial models, capturing much of the spatial variation in redd densities along a longitudinal gradient. In contrast, the predictor which merely described anchor ice presence (bel) was not in the top models. Thus, direct effects of anchor ice on early-life stages are potentially not as important to redd densities as the limitations that anchor ice pose for dispersal from Third Dam. As distance from Third Dam increases, the potential for anchor ice cover also increases, having a large negative effect on redd densities. Anchor ice has been shown to significantly affect trout behavior in other studies. In an Alberta, Canada river, the presence of anchor ice forced cutthroat trout into smaller areas of suitable habitat, resulting in large fish aggregations (Brown and Mackay, 1995). Within a Montana stream, both bull trout and cutthroat exhibited extensive movement in response to anchor break-up and refreezing (Jakober et al., 1998). We documented the potential for anchor ice to restrict access to spawning gravels, a pattern that has not been previously described in other research. This phenomenon could be further explored be documenting movements of brown trout during the spawning season in relation to anchor ice cover.

Other factors not included in our modeling efforts may have also affected redd densities, including unmeasured habitat factors, and/or biotic resistance by native Bonneville cutthroat trout, which exhibits high densities in upstream reaches of the River. Biotic resistance, which describes the ability of a native community to combat invasion pressure as a result of higher densities or competitive ability, may be particularly important to the spread of exotic species such as brown trout (Baltz and Moyle, 1993). Nevertheless, our best models captured nearly 70% of the variation in redd densities, highlighting the potential importance of several predictors, including distance from source areas, trends in anchor ice distribution, and gravel availability.

Our results indicate that remotely-derived stream power can be used as a surrogate for field estimates of unit stream power, when the goal is to broadly estimate areas of spawning gravel accumulation. In general, models which included remote stream power had similar predictive power as models which included field stream power. Even so, much error existed in the relationship between field and remote stream power estimates. This error can be largely attributed to error in the slope portion of the calculation. Other research has demonstrated that GIS-methods can overestimate slopes by 21 to 68% (Isaak et al., 1999). In this study, error in estimating slopes ranted from 20% (high slopes) to up to 100% (low slopes). Estimates of slope varied greatly between field and remote measures, which we attribute to errors in estimating elevation remotely. While vertical accuracy of elevation measures with the GPS are +/- 15 mm, the accuracy of elevation estimates for 10-m DEMs is much higher due to the presence of trees and other features on the landscape. Error in the vertical component of 10-m DEMS can be as high as 2.4 m (Gesch et al., 2002). Further loss of precision in elevation estimates can be attributed to lower spatial resolution of the 10-m DEMs used. Therefore, based on the amount of error, our approach would not be appropriate for estimating locations of gravel accumulation in low-elevation terrain. Nevertheless, estimates of unit stream power could be used to estimate broad-scale trends in gravel accumulation in river systems with more-varying and higher-

elevation terrain, such as between low-gradient study reaches located near Third Dam and high-gradient reaches near the Beaver Creek confluence. In the future, higher-resolution data could improve the accuracy of remote slope estimates and the applicability of this type of analysis (McKean et al., 2008).

Overall, our results demonstrate that a range of factors are responsible for the low redd densities present in the upstream portion of the Logan River, but that the general distribution of redds can be predicted based on a small suite of abiotic habitat and propagule pressure-related factors in this system. In order to further evaluate the influence of competing explanatory factors for brown trout invasion success, similar research would be necessary in study areas differing in the spatial distribution of temperature and other habitat characteristics. The same patterns of brown distributions are often observed along longitudinal gradients (Bozek and Hubert, 1992; Weigel and Sorensen, 2001), potentially due to similarities in river channel characteristics occurring from upstream to downstream. Thus there is a need for similar research conducted in riverine systems with alternate geomorphic arrangements, including those characterized by a range of elevations, stream sizes, and stream gradients (e.g., New Zealand, southern U.S.A., and the Oregon Cascades mountain range). Better knowledge of the history of the locations and intensity of brown trout introductions (e.g. , in Westley et al. 2011), would also improve our understanding of how propagule pressure factors influences invasion success.

CONCLUSIONS

We conclude that invasion success of brown trout on the Logan River is likely limited by abiotic habitat factors potentially affecting both early-life stages and adult brown trout, in conjunction with propagule pressure factors. In particular, the combination of abundant spawning habitat and ideal average temperature conditions in and near the impoundment contribute to extremely high brown trout spawning and adult densities and provides a source of brown trout to

upstream reaches. The apparent decrease in invasion and establishment success of brown trout with increasing distance upstream appears to be driven by distance from this high-density source area, the presence of anchor ice, and by overall gravel availability.

Such research could be used to inform management objectives regarding brown trout. For example, in cases where native trout conservation is a top priority, creation of physical barriers could limit brown trout invasion from source areas (Fausch et al., 2009). Further, changes in anchor ice cover due to climate change could be used to help explain the upstream movement of brown trout populations. In the Logan River, the upstream portion of river continues to be an important stronghold for native Bonneville cutthroat trout, due, in part, to habitat constraints on brown trout. Our research provides an example of how brown trout have successfully invaded a river system by dispersing from suitable sections of habitat, and how the spatial arrangement of this habitat and proximity to source areas is likely contributing to the altitudinal zonation pattern.

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CHAPTER 4

EXOTIC BROWN TROUT PREDATION ON NATIVE MOTTLED SCULPIN: THE CASE OF A NOVEL PREDATOR

ABSTRACT

While competitive interactions between invasive brown trout (*Salmo trutta*) and native fishes are well-established, the extent and degree of exotic brown trout predation on native fishes is less well understood. We evaluated abiotic habitat factors determining the distribution of native mottled sculpin (*Cottus bairdi*) and the potential for exotic brown trout predation on mottled sculpin in the Logan River, Utah, USA. Sculpin abundance was significantly correlated with physical variables describing median substrate size (+), width (+), and gradient (-), while brown trout abundance was significantly correlated with temperature variables, including average (+) and summer temperatures (+). In reaches where the two species co-occurred, we found sculpin in 0% of age one, 8% of age two, and 39% of age three and older brown trout diets. Sculpin comprised an average of 0%, 6%, and 30% of the diet contents of these age classes, respectively. These high rates of predation on sculpin contrasted with low rates of cannibalism on smaller brown trout and other salmonids observed in reaches with low sculpin densities. Brown trout selectively preyed on sizes of sculpin smaller than predicted by both gape limitations and availability in the environment. A typical age-three brown trout consumed up to 35 sculpin per year, resulting in up to 2000 sculpin consumed per year in a 2000 m^2 reach. Although native brown trout and sculpin commonly co-occur within the native range of brown trout, these results indicate that exotic brown trout represent a novel predator on native sculpin in this system. Such high rates of piscivory may ultimately affect the population structure and viability of sculpin populations on the Logan River and elsewhere where the two species co-occur.

INTRODUCTION

Success of an invasive species depends on both traits of the invasive species and characteristics of the invading environment (Kolar and Lodge, 2001). The ability to occupy a broader niche space than native species is a common trait held my many successful invaders (Vazquez et al., 2006). Species that have broad feeding niches can establish high densities and biomass by consuming either a broader range of prey, or more energetically-beneficial prey sources, thus outcompeting comparable native species characterized by a narrower feeding niche (Simon and Townsend, 2003) and altering the population dynamics of native prey communities (Sakai et al., 2001).

Brown trout (*Salmo trutta*), one the world's most successful invasive species (McIntosh et al., 2011), exhibits relatively high plasticity in diet, including the potential to shift to piscivory when prey fish are present. Based on optimal foraging theory, fish should shift their diets to eat more fish when higher densities of fish prey are available (Pyke, 1984). As a result, most trout species are opportunistic feeders and many become piscivorous at large sizes (Mittelbach and Persson, 1998; Keeley and Grant, 2001). However, within their introduced range, brown trout may consume more fish than their native counterparts of a similar size (McHugh et al., 2008). The highly piscivorous-nature of brown trout diets in their introduced range (McIntosh, 2000; Macchi et al., 2007) appears to contrast with diets of brown trout throughout much of the species native range, where even larger individuals feed primarily on drifting invertebrates (Rincon and Lobon-Cervia, 1999; Montori et al., 2006; Budy et al., *in review*). The mechanisms contributing to this lack of diet shift are largely unexplored but may be related to confined overlap in habitat use between brown trout and prey in Eurasian streams (Brown, 1991), or simply low densities or absence of prey fish.

Fish represent a higher-energy prey resource compared to invertebrates, resulting in faster growth and condition for piscivorous brown trout. Elliott and Hurley (2000) demonstrated that a change in diet from fish to invertebrates not only increases energy intake, but also increases the efficiency of energy conversion into growth by approximately 25%. The optimal temperature for trout feeding on fish may also be higher than when feeding on invertebrates, resulting in an even greater potential for growth (Elliott and Hurley, 2000). In addition to increased growth and condition, piscivorous trout often attain sexual maturity earlier than their non-piscivorous counterparts (Jonsson et al., 1984). The presence of small prey fish may result in brown trout becoming piscivorous at an early age, because they are less restricted by gape limitations (Keeley and Grant, 2001). Overall, a combination of ideal temperatures and abundant prey fish can contribute to increased trout growth and reproduction.

When in sympatry with other trout species, brown trout are typically superior competitors. For example, in a Michigan stream, native brook trout (*Salvelinus fontanalis*) chose locations with more favorable water velocities and canopy cover after the removal of brown trout (Fausch and White, 1981). Similarly, in experimental enclosures, Rio Grande cutthroat (*Oncorhynchus clarki virginialis*) individuals shifted their feeding niches to consume less-energetic prey in the presence of brown trout (Shemai et al., 2007). On the Logan River, Utah, the condition and growth of native Bonneville cutthroat trout (*Oncorhynchus clarki Utah*) decreased in experimental enclosures with brown trout while, conversely, brown trout performance was unaffected (McHugh and Budy, 2005). Finally, in experiments which explicitly considered the effects of fish size, white-spotted char (*Salvelinus leucomaenis leucomaenis*) occupied less suitable positions in the water column when in sympatry with brown trout of a smaller size (Hasegawa et al., 2004). In these examples, trout displaced by exotic brown trout were native species of conservation concern. Because brown trout are typically superior

competitors, all else equal, any size advantage gained via piscivory should add to their competitive advantage over other trout species.

As a predator, brown trout may also have widespread impacts on native communities. Brown trout predation has been attributed to the decline of native fish in New Zealand and Patagonia (McIntosh, 2000; Macchi et al., 2007). In some New Zealand streams, native galaxid fish are now restricted to headwaters located upstream from waterfalls, where they can avoid predation by brown trout (Townsend and Crowl, 1991). Similarly, in streams in Virginia, densities of native fish are negatively correlated with the presence of brown trout (Garman and Nielsen, 1982). Further, the impacts of brown trout predation may cascade through entire stream ecosystems. For example, the presence of exotic brown trout has resulted in the reduction of algae-eating macro-invertebrates and higher algal biomass within some New Zealand streams (Garman and Nielsen, 1982). However, despite the potential negative effects of brown trout predation on individual species, communities, and ecosystems, studies of the impacts of brown trout predation are rare compared those investigating competitive interactions.

In this study, we explored the potential for exotic brown trout predation on native mottled sculpin on the Logan River, Utah. The study is contained within a long-term research project aimed at both monitoring populations of a critical population of native Bonneville cutthroat trout as well as documenting impacts of brown trout to the native fish community. Previous research suggests that brown trout on the Logan River consume more fish than native Bonneville cutthroat trout of a similar size (de la Hoz Franco and Budy, 2005; McHugh et al., 2008), which may contribute to the species' competitive advantage. Mottled sculpin is the only non-salmonid prey species occurring in this system and commonly co-occurs with brown trout (Bailey, 1952; Quist et al., 2004) throughout the Intermountain West. The mottled sculpin (hereafter sculpin) is almost exclusively benthic, native and, in the western U. S.A., is often associated with mid-gradient, coldwater streams with temperatures above 10°C in the summer (Quist et al., 2004).

We sought to evaluate the potential for exotic brown trout predation on sculpin at study reaches throughout the Logan River watershed, Utah, by investigating:

i) the extent of co-occurrence of native sculpin and exotic brown trout,

ii) habitat factors potentially influencing co-occurrence

iii) the contribution of sculpin to the diet of different size/age classes of brown trout, and

iv) the potential for individual and population-level consumption of brown trout on sculpin, using bioenergetics.

METHODS

Study area

The Logan River is located in southeast Idaho and northern Utah. The headwaters originate in the Bear River range, and the river drains into the Bear River and then into the Great Salt Lake. The climate is cold and snowy in winter (January air temperature: low, -9°C; high, 0°C,mean precipitation 4.0 cm) and hot and dry in summer (July air temperature: low, 15°C, high 31°C, mean precipitation 1.6 cm). Due in part to the presence of springs, average summer water temperatures are near 10°C. The hydrograph is characterized by spring runoff snowmelt events and a relatively low ratio of peak flow to baseflow, due to abundant karst features in the watershed. Within the study area, discharge data collected hourly at long-term study sites demonstrates that average discharge in the mainstem river ranges from 2.16 m^3/s at Franklin Basin to 4.76 m^3/s near the Logan River USGS gauge located at the downstream portion of the study area. Average tributary discharge ranges from 0.105 m^3/s for the tributary of Spawn Creek to 0.796m^3/s at the mouth of Temple Fork Creek. In addition to native Bonneville cutthroat trout, exotic brown trout, and sculpin, the river also contains mountain whitefish (*Prosopium williamsoni*), and small numbers of exotic brook trout (*Salvelinus fontinalis*) and stocked rainbow

trout (*O. mykiss*) in isolated sections. Exotic brown trout were first introduced to the study area in the early 1900's.

Within the study area, the Logan River is relatively pristine, with the exception of highly localized effects of grazing-related habitat degradation in some headwater reaches, the presence of three dams and associated habitat alteration near the city of Logan, and a canyon road adjacent to the river. A more detailed description of the study area, including information describing the fish community, is available in Budy et al. (2008) and Chapters 1 and 2 of this dissertation.

Brown trout and sculpin co-occurrence

We collected brown trout abundance data at twelve reaches in the Logan River watershed as part of a long-term study, occurring from 2001 to 2011. Our study reaches encompassed more than 50 stream kilometers of the Logan River and ranged from 1352 to 2023 meters in elevation (Figure 4.1). Each study reach was approximately twenty channel widths in length. Study reaches included eight long-term reaches, sampled annually, as well as four supplementary reaches sampled in a subset of years. Long-term reaches included Third Dam, Twin Bridges, Forestry Camp, Redbanks, Franklin Basin, and the tributary reaches of Right Hand Fork, Spawn Creek, and Temple Fork. Supplementary reaches included Bridger, Woodcamp, Beaver Creek, and Temple Fork Upper reaches. The reaches of Bridger and Third Bridges are located between two dams on the river, while the Lower Logan reach is located downstream of these dams.

Brown trout abundance data was collected in July or early August, at both long-term and supplemental sampling reaches. We performed all sampling using a backpack (tributaries) or canoe-mounted (main river) electrofishing unit. We marked captured brown trout > 120 mm at each reach during each survey, using individually coded, T-bar anchor tags and site-specific colors. We also measured lengths and weights of each trout captured. Further information about collection methods can be found in Budy et al. (2008). We estimated brown trout population

abundance using a three-pass, closed, generalized maximum-likelihood removal estimator (Peterson et al., 2004), in which a block net was placed at the upstream and downstream end of each reach. We estimated mean brown trout abundance for each reach by averaging

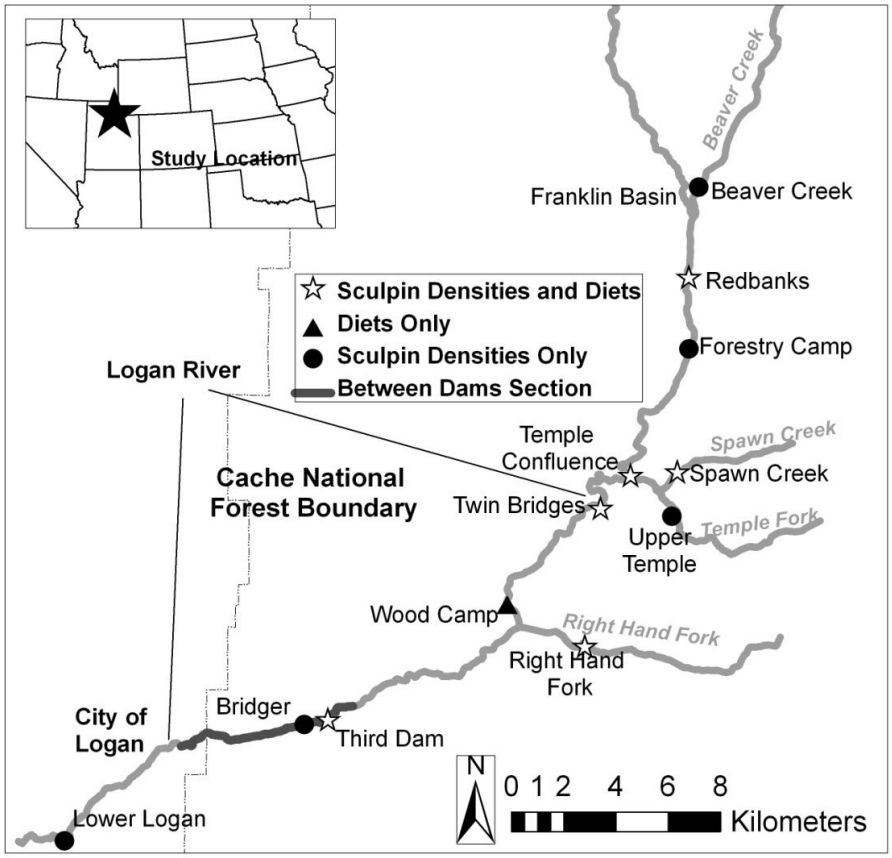

Figure 4.1. Study reaches on the Logan River, Utah

abundance data across years (2002-2011) and average densities by dividing average abundance by the area of the reach.

During the years 2008-2011, we also collected sculpin at long-term and supplementary survey reaches during summer surveys. We estimated sculpin abundance for each reach and year similar to above using a three-pass removal estimator. We recorded lengths and weights of the

first 100 sculpin collected at each reach. In several cases where a three-pass depletion did not occur, we combined the first two passes, and used a two-pass depletion method. We estimated mean sculpin abundance by averaging abundance data across years (2008-2011) and average densities by dividing abundance by the area of the reach.

Abiotic habitat characteristics potentially affecting co-occurrence

We characterized abiotic habitat characteristics annually during long-term and supplemental reach surveys, in order to evaluate factors influencing brown trout and sculpin co-occurrence (Table 4.1). We selected abiotic habitat variables based on previous research highlighting their importance in determining sculpin (Maret, 1997; Quist et al., 2004) or brown trout (Bozek and Hubert, 1992; Rahel and Nibbelink, 1999) distributions. Abiotic habitat variables evaluated included wetted width, gradient, D_{50} (hereafter referred to as median substrate size), pH, conductivity, average temperature, summer temperature, and winter temperature. We estimated wetted width (m) at ten equally spaced transects, averaged to obtain an estimate for the reach. We calculated gradient by dividing the change in water surface elevation in each reach by the length of the reach. We estimated median substrate size from pebble counts conducted at these equally-spaced transects, in which a gravelometer was used to measure substrate size of ten randomly selected particles at each transect. We measured conductivity and pH using a YSI probe. To take advantage of multiple years of data for wetted width, gradient, median substrate size, conductivity, and pH, we averaged across years to obtain an estimate for each reach. We based temperature estimates on hourly data collected using HOBO loggers deployed at each in 2010, and averaged across the time period of interest. These estimates included annual temperature (1 Jan –31 Dec), summer temperature (1 July –31 Aug), and winter temperature (1 Jan–28 Feb ; 1 Nov–31 Dec). We used spearman correlation coefficients, estimated using Program R (R Core Development Team, 2011), to evaluate the magnitude and significance

($p<0.10$) of correlations between abiotic habitat characteristics and brown trout and sculpin densities.

Table 4.1. Average reach characteristics, estimated from summer long-term and supplemental sampling events.

Reach	width (m)	gradient	D_{50} (mm)	pH	cond-uctivity ($\mu S/cm^{3)}$	average temp (°C)	summer temp (°C)	winter temp (°C)
Lower Logan	12.1	0.005	42	8.23	482	8.41	14.35	3.82
Bridger	10.2	0.006	80	7.64	338	5.61	11.24	3.1
Third Dam	10.2	0.01	105	7.64	338	5.61	11.24	3.1
Twin Bridges	13	0.009	90	8.28	350	5.74	11.05	2.22
Forestry Camp	11.6	0.015	163	8.44	322	5.51	10.87	1.55
Redbanks	9.8	0.02	72	8.41	323	5.19	9.77	1.59
Franklin	8.4	0.026	100	8.26	293	4.7	9.17	1.99
Right Hand Fork	3.56	0.027	26	8.19	393	9.7	11.04	8.77
Temple Fk Conf	6.7	0.043	50	8.31	338	5.86	10.38	2.78
Temple Fk Up	6.7	0.027	48	8.28	319	5.2	9.05	2.37
Beaver Creek	5.62	0.015	48	8.26	293	5.03	9.5	1.99

Consumption of sculpin by brown trout

We merged diet data collected during multiple sampling events to evaluate the degree of piscivory and the overall contribution of sculpin to the diet of brown trout at multiple reaches. We collected diet data from July through September, during the years 2001-2011. During these sampling events, we used a combination of lethal dissection and non-lethal gastric lavage to extract stomach contents. We used a dissecting microscope to classify individual items to order, and we weighed (wet weight, g) and measured (mm) all fish in the stomach contents.

We compared sculpin sizes collected during electroshocking surveys to sculpin sizes in brown trout diets, and to published gape limits for brown trout. We estimated length-frequency distributions for sculpin from cumulative length data collected across all sample years (2008-2011) and across sample reaches where the majority of diet data was collected (Bridger, Third Dam, Twin Bridges). We estimated average sizes of each age class of brown trout based on a

combination of mark-recapture, length-frequency, and otolith data, where age 0 was 0-99 mm, age one was 100-179 mm, age two was 180-259 mm, and age three was 260 mm and longer. We determined the total length of sculpin that could be consumed based on a relationship between brown trout size and gape limitation found in Ebner et al. (2007). In our calculations, we estimated gape limitations based on sculpin body depth, but we a used relationships between body depth and total length (Maughan, 1978) to develop our equation. The resulting formula for maximum length of sculpin consumed in relation to brown trout size was:

$$Sculpin\ Total\ Length\ (mm) = 0.66 * Brown\ Trout\ Total\ Length\ (mm) - 34.53$$

We evaluated the potential shift to a diet containing sculpin by estimating the prevalence of piscivory and magnitude of fish in diets. We estimated the prevalence of piscivory for each reach as the percentage of brown trout in each age class containing a fish in its stomach contents. We estimated the magnitude of fish in diets as the mean percentage wet weight of sculpin in the digestable stomach contents of individual brown trout in each age class, with 95% confidence intervals. We only performed these calculations if diet data exceeded four individuals within a reach and size class. We compared the prevalence and magnitude of piscivory in reaches with sizable sculpin densities (≥ 0.05 sculpin/m^2 ; n=186) to estimates for reaches containing low densities, or where sculpin were absent (< 0.05 sculpin/m^2; n=168).

Potential for individual and population-level consumption on sculpin

We used the Wisconsin bioenergetics approach (Hanson et al., 1997) to model the potential annual consumption of sculpin by individual brown trout and at the population (reach) level. For this analysis, we modeled consumption in reaches where the most abundant diet data were available, including Third Dam, Twin Bridges, Woodcamp, and Temple Fork. We based physiological parameters on laboratory-derived data for brown trout (Dieterman et al., 2004). For

all model runs, we modeled the average thermal history at a daily timestep from 10 Aug 2010 to 9 Aug 2010. We chose the 10 Aug date because it approximates the date of the annual surveys each year, during which brown trout abundance data is collected. We estimated average daily temperatures from hourly data collected using HOBO temperature loggers deployed at each reach. We estimated growth rates of brown trout (g/ day) in each age class from weights (g) measured during mark-recapture surveys (Budy et al. 2008). To estimate the percentage of sculpin and brown trout in diets, we used the July-September diet data collected from 2001 to 2011. Although seasonal variation in diet certainly occurs, preliminary simulations indicated that the majority of growth (~ 70 %) for brown trout on the Logan River occurs during July-September. Based on inputs of thermal regime, diets, and brown trout growth as described above, we used the bioenergetics model to estimate the potential annual number of sculpin consumed by an average brown trout in each reach and size class.

We estimated population-level consumption by scaling this individual-level consumption by the number of brown trout up to the 2000 m^2 area. Brown trout growth information was not available for the Woodcamp reach due to a lack of mark-recapture data. Therefore, we assumed growth of brown trout in this reach to be similar to that of the Twin Bridges Reach, the nearest upstream reach which demonstrates similar temperatures and brown trout densities.

RESULTS

Brown trout and sculpin co-occurrence

Sculpin co-occurred with brown trout at many sample reaches (Figure 4.2). We recorded the highest average densities of both brown trout (~0.163 individuals/m^2) and sculpin (0.604-0.913 individuals/m^2) within a section between two small impoundments (Bridger and Third Dam reaches). Other mainstem reaches where we recorded both species included Lower Logan, Twin Bridges, Forestry Camp, and Red Banks. However, we recorded extremely low brown trout

densities at the Red Banks (0.004 individuals/m^2) and Forestry Camp (0.003 individuals/m^2) reaches, and we recorded low sculpin densities at the Lower Logan Reach (0.028 individuals/m^2). In addition, we found sculpin to be nearly absent (0.004 individuals/m^2) from the Temple Confluence reach, which contained relatively high (0.121 individuals/m^2) densities of brown trout. We observed intermediate densities of sculpin at the most upstream reaches of Franklin Basin (0.073 individuals/m^2) and Beaver Creek (0.088 individuals/m^2), where brown trout were absent. We observed no sculpin in the tributary reaches of Spawn Creek, Upstream Temple Fork, and Right Hand Fork, where we observed intermediate (0.033 individuals/m^2 in Spawn Creek) to high (0.622 individuals/m^2 in Right Hand Fork) densities of brown trout.

Abiotic habitat characteristics potentially affecting co-occurrence

Relative densities across years were similar between reaches, with the exception of high densities measured at the Forestry Camp in 2009, which were up to ten times higher than those measured in 2008 and 2010. This 2009 measurement was determined to be an outlier (Grubbs, 1969), and we omitted it from the estimate of density for the Forestry Camp reach.

Interactions between abiotic variables and sculpin densities in this system are complex and nonlinear (Figure 4.3). We observed strong, significant correlations ($p< 0.10$) between sculpin densities and our variables describing physical habitat including wetted width, gradient, and median substrate size. In contrast, we observed strong, significant correlations ($p<0.10$) between brown trout densities and average, maximum, and minimum temperature, as well as conductivity and pH (Table 4.2).

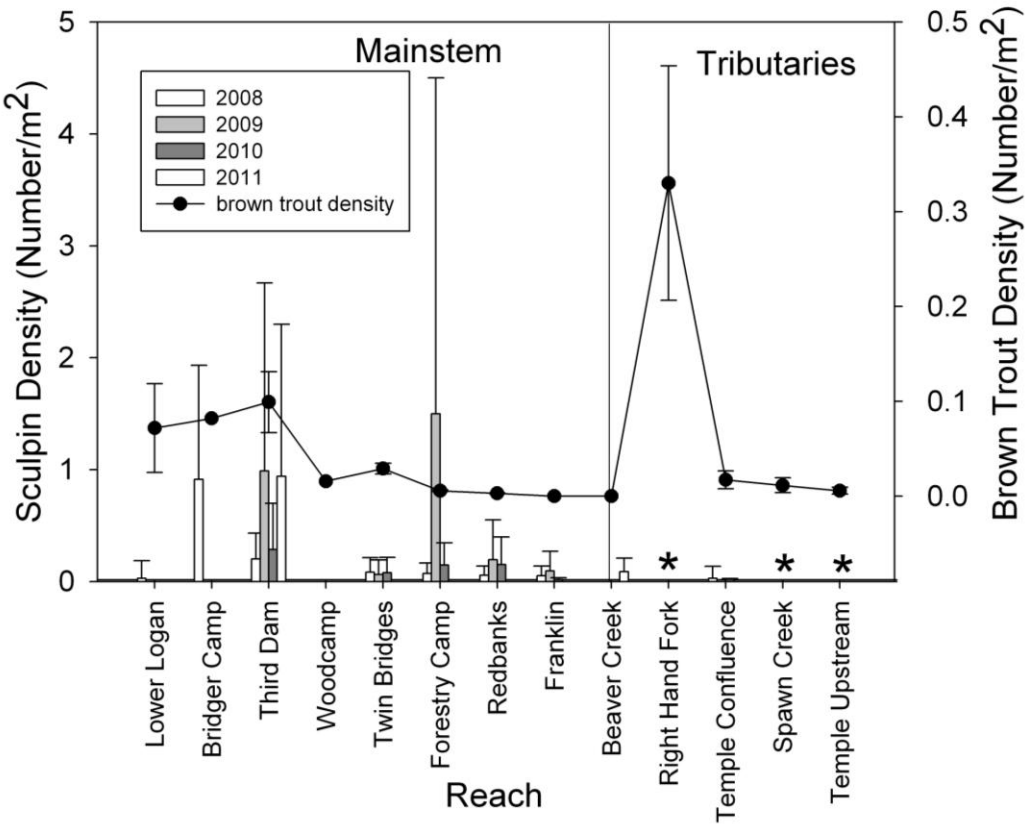

Figure 4.2. Average sculpin densities (with 95% confidence intervals), by year, in relation to average brown trout densities across years (with 95% confidence intervals) at study reaches on the Logan River, Utah. Asterisks indicate that no sculpin were collected in the reach.

Consumption of sculpin by brown trout

Brown trout consumed smaller sizes of sculpin compared to those available in the environment, despite the presence of many large brown trout (Figure 4.4). Based on the sizes of sculpin present and the published gape limits for brown trout, we predicted that a typical brown trout in the Logan River should be physically able to consume small (20 mm-50 mm) sculpin at age one, medium-sized (50 mm-120 mm) sculpin at age two, and all sizes of sculpin available (20 mm-180 mm) by age three. However, we did not find sculpin greater than 100 mm in brown trout diets, even though these sizes were found in the presence of large brown trout (Figure 4.4).

Table 4.2. Spearman correlation coefficients between brown trout densities and habitat variables (D_{50}=median grain size, grad=gradient, cond=conductivity, avgtemp=average temperature, win temp = winter temperature, sum temp=summer temperature). Bolded values indicate $p < 0.10$.

	sculpin	brwns	D_{50}	width	grad	pH	cond	avg temp	win temp	sum temp
sculpin	-1.00	-0.12	**0.78**	**0.75**	**-0.67**	0.05	-0.14	-0.38	-0.37	-0.38
browns	-0.12	1.00	-0.30	-0.01	0.01	**-0.80**	**0.61**	**0.65**	**0.76**	**0.50**
D_{50}	**0.78**	-0.30	1.00	**0.68**	-0.41	0.31	-0.27	**-0.53**	**-0.64**	0.07
width	**0.75**	-0.01	**0.68**	1.00	**-0.82**	0.03	0.04	-0.09	-0.27	**0.54**
grad	**-0.67**	0.01	-0.41	**-0.82**	1.00	0.15	0.04	0.07	0.05	**-0.63**
pH	0.05	**-0.80**	0.31	0.03	0.15	1.00	**-0.60**	**-0.58**	**-0.84**	**-0.59**
cond	-0.14	**0.61**	-0.27	0.04	0.04	**-0.60**	1.00	**0.85**	**0.68**	**0.66**
avgtemp	-0.38	**0.65**	**-0.53**	-0.09	0.07	**-0.58**	**0.85**	**1.00**	**0.82**	**0.66**
wintemp	-0.37	**0.76**	**-0.64**	-0.27	0.05	**-0.84**	**0.68**	**0.82**	**1.00**	**0.55**
sumtemp	-0.38	**0.50**	0.07	**0.54**	**-0.63**	**-0.59**	**0.66**	**0.66**	**0.55**	**1.00**

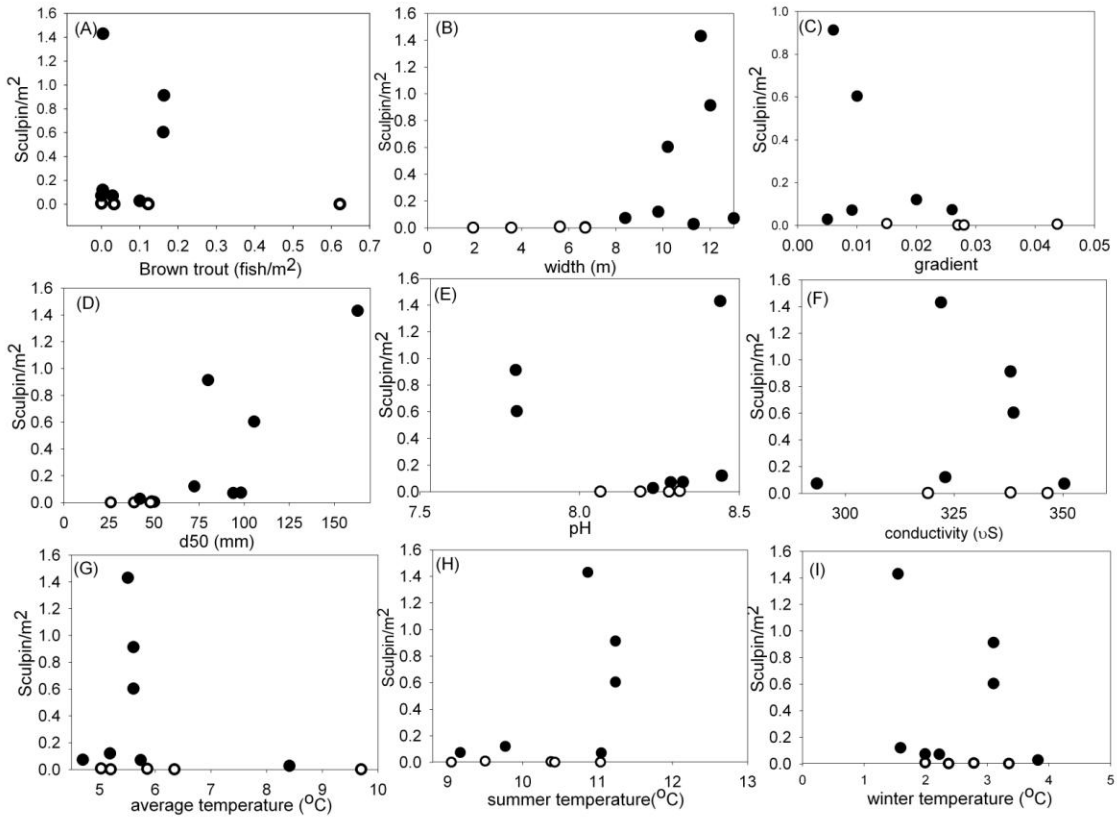

Figure 4.3. Sculpin densities in relation to brown trout densities and eight habitat variables (A-I) measured at twelve study reaches. Dark circles: mainstem; open circles: tributaries.

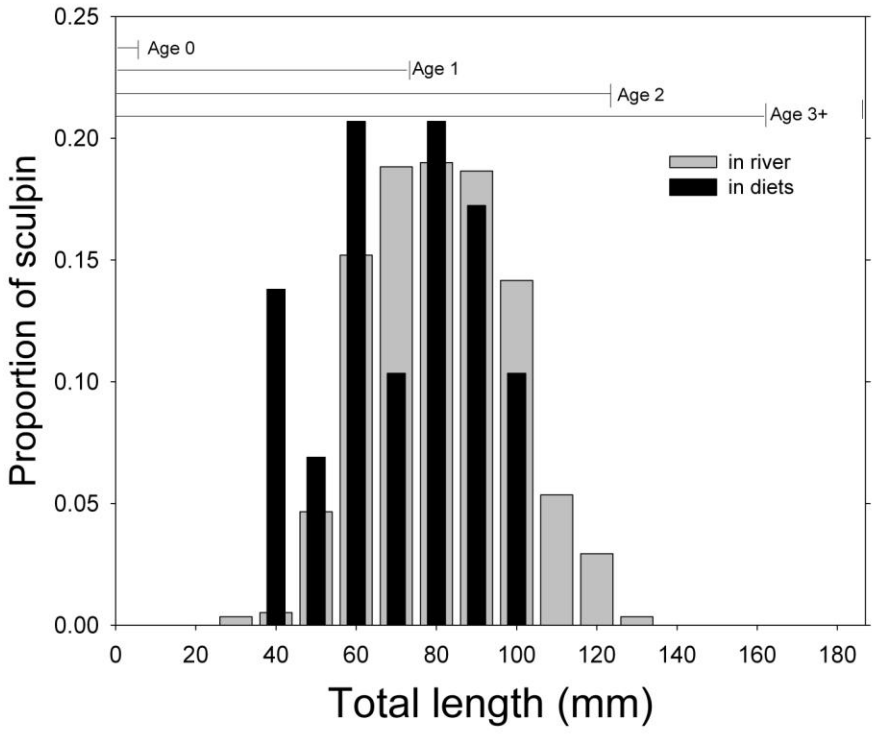

Figure 4.4. Length frequency histograms of sculpin availability across reaches compared to those found in diets of brown trout on the Logan River and the predicted size of sculpin that could be consumed by brown trout in each size class.

The sizes of sculpin recorded in brown trout diets were also considerably less than the theoretical gape limitation for brown trout of a certain size, as estimated using Ebner et al. (2007) (Figure 4.5). Although the size of sculpin consumed increased with brown trout size, this relationship was not significant ($F_{1,55}$=2.26, p=0.138). Further, the slope of the relationship between brown trout size and the size of sculpin consumed (slope=0.138) was less than the theoretical relationship predicted by gape limitations (slope = 0.66).

In addition, we documented that a large number of brown trout < 50 mm were found in diets, even though few fish of these small sizes were collected in river surveys. Based on the length-frequency histogram, we estimate that fish < 50 mm may represent recently emerged, age-0 sculpin.

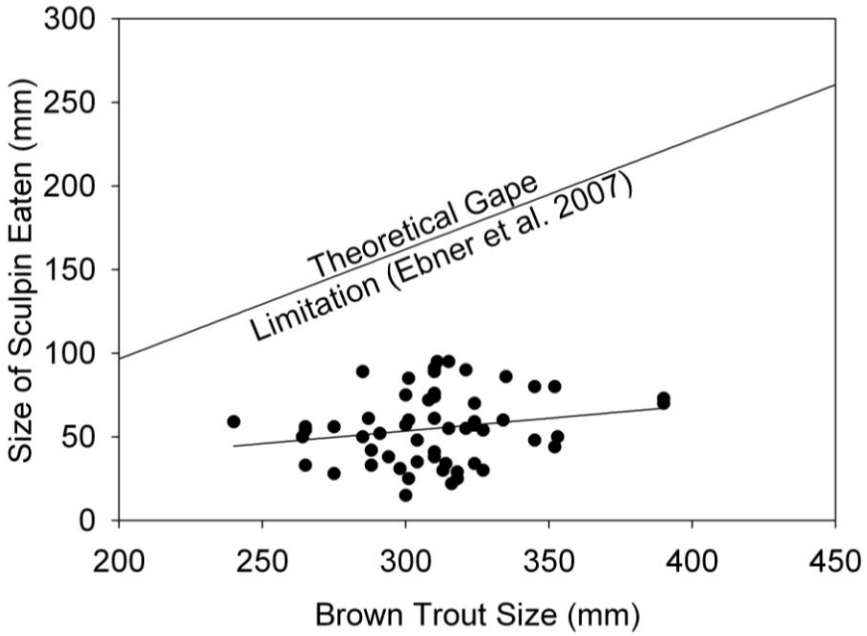

Figure 4.5. Length of sculpin consumed by brown trout compared to the theoretical gape limitation for brown trout of a certain size.

Brown trout predation varied by fish age and reach (Figure 4.6A). As much as 25% (Third Dam) of age two and 60% (Redbanks) of age three brown trout had sculpin in diets. Within reaches containing sculpin, the only non-sculpin fish prey included a brown trout found in the diet of an age three brown trout at the Twin Bridges reach. The percent of sculpin in diets was as high as 17% for age two brown trout (Third Dam) and 40% for brown trout over age three (Woodcamp). Within-reach variation in diets was also high, with the percentage of sculpin in diets ranging from 0-100% for both age two and age three and older brown trout.

Within reaches containing sculpin (Third Dam, Woodcamp, Twin, Forestry, Redbanks), brown trout predation was widespread. We found no sculpin in the diets of age one brown trout (n=57). However, we recorded sculpin in an average of 8% (n=36) of age two and 39% (n=93) of

age three brown trout (4.6A). In contrast, the mean percentage of age three and older brown trout that consumed other fish species (in this case, brown trout) across all reaches containing sculpin was 1%. Sculpin also comprised a large portion of the diets of piscivorous brown trout (Figure 4.6B). An average of 6% (age two) and 30% (age 3+) of the stomach contents of individual brown trout contained sculpin (Figure 4.6B), but the degree of piscivory varied by reach. The average percent of sculpin in the diet of piscivorous individuals was 74% for both age two and age three brown trout.

In contrast to reaches containing high densities of sculpin, consumption of fish prey was extremely low in reaches with no (Right Hand Fork, Upper Temple) or extremely low (Temple Confluence) sculpin densities. We found fish in 0% of age one (n=30), 0% of age two (n=46), and only 6% of age three (n=92) brown trout. Consumption of fish in these reaches consisted of a single sculpin eaten at the Temple Confluence Reach and five small brown trout consumed at the Right Hand Fork reach.

Potential for individual and population-level consumption of sculpin

According to our bioenergetic simulations, brown trout consumption rates on sculpin were high within reaches where the species co-occurred (Table 4.3). Results of bioenergetic models illustrated that a typical age two brown trout consumes three to thirteen sculpin a year, while a typical brown trout over age three potentially consumes one to 35 sculpin a year, depending on the reach. When considering the abundance of brown trout at each reach, annual consumption by age two brown trout potentially ranges from 51 to 2510 sculpin per reach, while consumption by age three brown trout ranges from 18 to 837 sculpin per reach.

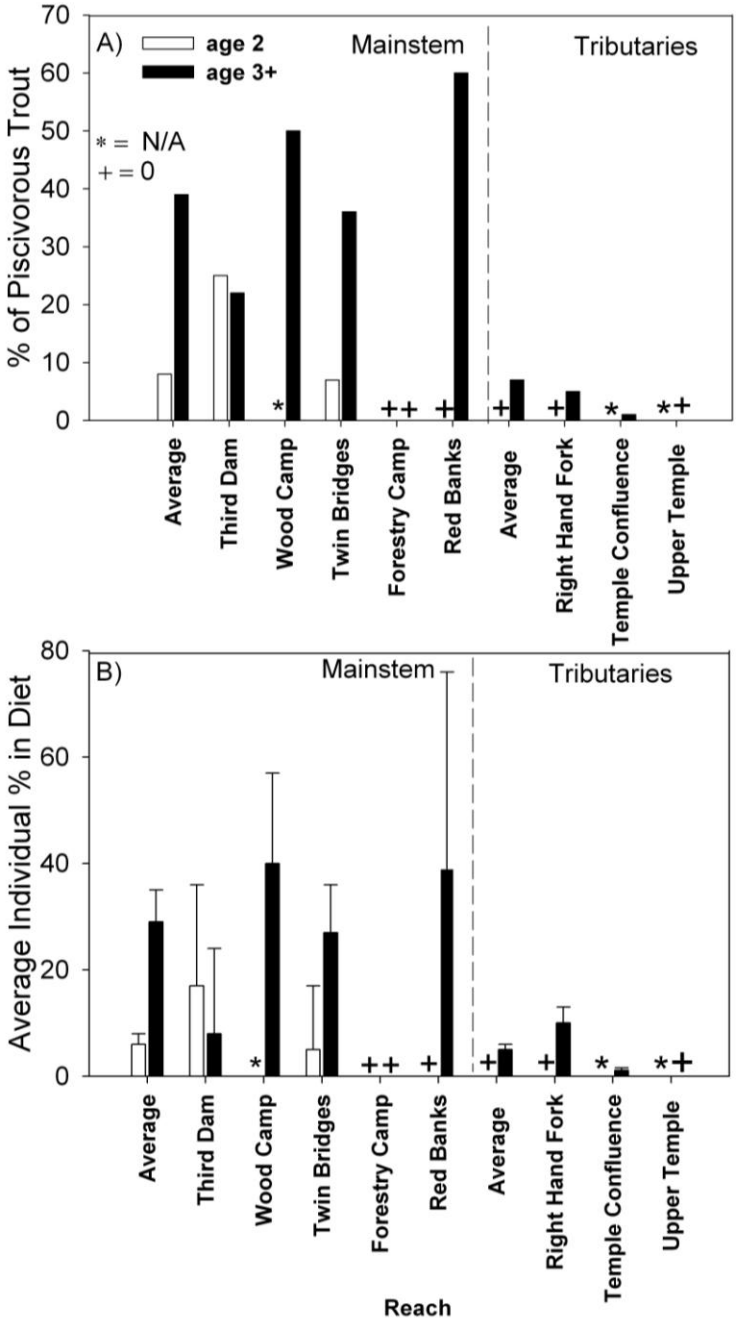

Figure 4.6A,4.6 B. The % of piscivorous brown trout in each reach (A), and the average percentage of fish eaten by individual brown trout in each reach , with 95% confidence intervals (B). Crosses indicate that no fish were found in diets, while asterisks indicate that the sample size was too small (n<5) to obtain an estimate.

Table 4.3. Parameters and results for bioenergetic modeling runs, illustrating the high number of sculpin potentially consumed per year at the individual and population levels and compared to the number of sculpin estimated for each reach. Double asterisks (**) denote that not enough data (n<5) was available for that size class to perform the calculation.

Reach	Age Class	% sculpin eaten	% inverts eaten	Avg. Sculpin Wt. (g)	Initial Wt (g)	End Wt (g)	# sculpin/ individual	# sculpin/ population
Third Dam	Age 2	17	83	6.58	125.16	216.64	13	2510
	Age 3+	8	83	6.58	216.64	321.67	8	837
Wood Camp	Age 2	**	**	**	**	**	**	**
	Age 3 +	40	60	8.11	229.45	397.35	42	672
Twin Bridges	Age 2	5	95	8.11	127.51	229.45	3	51
	Age 3+	27	73	8.11	229.45	397.35	35	446
Temple Fork	Age 2	0	**	15.65	**	**	**	**
	Age 3+	2	98	15.65	170.88	291.5	1	18

DISCUSSION

The invasion success of brown trout across their introduced range has been attributed to their generalist habitat requirements compared to native trout species (Simon and Townsend, 2003), including the ability to thrive given a range of temperature and other physical habitat conditions (Armstrong et al., 2003). We illustrated the potential for exotic brown trout to become piscivorous in the presence of high densities of native fish prey, which may also contribute to brown trout invasion success. In portions of the Logan River watershed where brown trout and sculpin co-occurred, sculpin comprised a significant portion of the diet and energy budget of brown trout. In places where sculpin densities were low, brown trout rarely consumed smaller

brown trout or other salmonids. These findings, coupled with past research showing comparatively lower piscivory by native cutthroat trout on sculpin (McHugh et al., 2008), indicate that introduced brown trout are a novel predator on native sculpin in this system, with the potential to influence sculpin population dynamics.

Research on the distribution and dynamics of mottled sculpin in the Intermountain West is generally lacking. Most notably, Bailey (1952) described the life history and ecology of the Rocky Mountain mottled sculpin (*Cottus bairdi punctulatus*) in the West Gallatin River, Montana. In that system, mottled sculpin were most abundant in riffle areas containing cobble and boulders and their primary food source was invertebrates. Further, mottled sculpin occurred in spring streams that were both wide and deep in research investigating the factors influencing the occurrence of both mottled and paiute sculpin (*Cottus beldingi*) in the Salt River Watershed in Idaho and Wyoming (Quist et al., 2004). Those streams were dominated by fine substrate, and supported high densities of brown trout; however, sculpin were absent from tributaries with low summer water temperatures and high-gradient reaches. Thus, one goal of our study was to further explore abiotic factors influencing sculpin densities within an Intermountain West river system, in order to better understand how a broad range of factors may influence distributions.

We recorded densities that were within the range of that reported by other research (McCleave, 1964). Our high-density estimates were also similar to that previously measured by Zarbock (1946) on the Logan River (~0.9 sculpin/m^2), but the location of sampling is unknown. It is important to note that sculpin abundance is usually underestimated due low to capture efficiencies (Zaroban, 2011). A large amount of error also existed in our estimates of sculpin densities, which could have been reduced with a greater number of passes. Our estimates of abundance can be best considered an index. Nonetheless, we were able to capture broad-scale differences in abundance which may be representative of many river systems in the Intermountain West which contain both sculpin and brown trout (a common assemblage; Burbank 2011).

Sculpin densities were highly correlated with predictor variables describing general stream geomorphology, indicating that factors affecting movement and physical habitat structure are important to the distribution of this highly benthic fish species. High gradients of tributary reaches may prevent sculpin from moving upstream; all of the tributary reaches which were not located at a confluence with the mainstem (e.g.,except Temple Confluence) contained no sculpin. Sculpin densities may also reflect an interaction between geomorphic and temperature variables. We observed that sculpin densities are high in the reaches between two dams (e.g, Bridger and Third Dam) where average temperatures are high and substrate size is relatively large. The substrate at Bridger and Third Dam reaches is considerably larger than some upstream reaches, which is potentially a result of canyon inputs and channelization activities. Sculpin densities at these reaches are much higher than at Franklin Basin, a reach characterized by relatively large substrates but less suitable temperatures (<10°C). Densities in these reaches are also higher than those observed in the Lower Logan, which is conversely characterized by suitable temperatures (>10°C) but relatively smaller, less suitable substrates.

Positive relationships between stream temperature and sculpin abundance have been observed in other systems (Maret, 1997; Quist et al., 2004), but the importance of median substrate size has received little attention. Large cobbles and small to medium-sized boulders provide sites for male sculpin to prepare nests (Bailey, 1952) as well as for the evasion of predators. The strong relationship between sculpin densities and channel characteristics, such as gradient and substrate size, could be used to explain patterns of sculpin abundance in other systems.

In contrast to sculpin, brown trout abundance was best predicted by temperature-related and water quality variables (namely pH and conductivity). Although pH and conductivity are sometimes correlated with temperature measurements (Maret, 1997; Soldner et al., 2004), past studies have generally shown weak relationships between these variables and brown trout

densities compared to temperature measurements (Jowett, 1992; Olsson et al., 2006). Temperature variables are among the most important for predicting brown trout abundance, yet other habitat factors may interact with temperature to affect brown trout densities (Rahel and Nibbelink, 1999). In this study, we did not observe strong relationships between selected habitat variables (gradient, width, median substrate size) and brown trout abundance. However, we did not include measures of variables such as pool-riffle and spawning gravel availability, which may also influence brown trout distributions on the Logan River (Heggenes et al., 2002). Nonetheless, our findings support other research illustrating that patterns of brown trout abundance are closely correlated to changes in temperature (Rahel and Nibbelink, 1999; Isaak and Hubert, 2004). We can, therefore, predict the portions of watersheds in which brown trout and mottled sculpin are most likely to co-occur. Based on our results, these include mid-gradient reaches with substrates generally larger than cobble-sized and with average temperatures greater than 10°C, but less than the upper thermal limit of brown trout. At much lower temperatures, we observed that both brown trout and sculpin abundance was low (e.g., Franklin, Forestry, Redbanks reaches). In contrast, when substrates were much smaller than cobble-sized (e.g., Lower Logan reach) or high gradients were present (e.g.,tributary reaches, including Temple Confluence, Upper Temple, Spawn Creek, and Right Hand Fork), sculpin abundance was low. Collectively, these results have implications for the growth and invasion success of brown trout in similar river systems, a success which may be facilitated by the consumption of mottled sculpin.

Our hypotheses of occurrence could be verified by further studying sculpin and brown trout distributions within other river systems in the Intermountain West. Using such an approach, Burbank (2011) recently demonstrated that factors best predicting sculpin densities included width and mean temperature, and were not necessarily related to maximum temperature or substrate size. These results do not necessarily reflect abiotic factors which limit mottled sculpin, however, because the aforementioned study considered combined densities of three

sculpin species. Species of sculpin demonstrate a wide range of habitat preferences (Maret, 1997; Quist et al., 2004). Furthermore, Burbank (2011) used a large regional database of available data, and abiotic factors affecting sculpin distributions at this broad spatial scale could differ from those affecting distributions within individual watersheds.

Even though previous research has indicated that brown trout distributions appear to strongly influenced by abiotic factors, and less so by biotic interactions (McHugh and Budy, 2006; Budy et al., 2008; Wood and Budy, 2009), our results indicate that piscivory may positively influence growth and reproduction of brown trout in reaches where environmental factors are suitable (Mittelbach and Persson, 1998; Jonsson et al., 1999). In a meta-analysis of prey sizes eaten by salmonids in waterbodies of varying sizes, brown trout residing in lakes grew faster than riverine brown trout because of the presence of smaller sizes and higher densities of fish prey. The presence of small prey allowed them to overcome gape limitations at an early age (Keeley and Grant, 2001). As a result, if high densities and small sizes of prey are present in river systems, brown trout have the potential to exhibit similarly high growth rates. Some of the highest estimates of brown trout densities and/or condition (de la Hoz Franco and Budy, 2005; Budy et al., 2008) on the Logan River have been recorded at reaches which also contain relatively high densities of sculpin (Third Dam, Twin Bridges). Growth and reproduction at these reaches is also potentially higher than in the absence of predation on sculpin, a pattern which may contribute to the competitive advantage of brown trout over cutthroat trout within these reaches (McHugh and Budy, 2005).

In this study, the sizes of sculpin consumed by brown trout on the Logan River were less than the maximum predicted by gape limitation and size availability. A similar preference for smaller piscine prey has been observed in other systems (Nilsson and Brönmark, 2000; Jensen et al., 2008) and may be related to a variety of factors, including increased handling time with increasing prey size, higher probability of capture success of small prey, and stomach volume

limitations (Truemper and Lauer, 2005). Although we observed the smallest size range (20-40mm) of prey in diets, these sizes were typically less abundant in stream surveys. This pattern may reflect a greater ability by these small sculpin to avoid capture by hiding in rock crevices (Zaroban, 2011). In addition, this pattern may be due to a lag in the time period between when sculpin were collected versus when the brown trout diet data was collected. Although the sculpin density data was collected in July and August, diet data was collected from August through November. An abundance of small mottled sculpin may allow brown trout on the Logan River to overcome gape limitations and convert to piscivory at an early age.

In this study, age-two fish (ranging in size from 180-259 mm) were the youngest to exhibit piscivory. Others have similarly observed a shift to piscivory in rivers for exotic brown trout occurring at either age two or three, and sizes ranging from 130-280 mm (L'Abée-Lund et al., 1992; Jonsson et al., 1999); however, the prevalence and magnitude of fish in diets can increase dramatically with fish size (Garman and Nielsen, 1982; Keeley and Grant, 2001). For instance, in a Virginia River, only 6% of brown trout < 280 mm consumed fish prey, while 28% to 100% of diets of large exotic brown trout (> 280 mm) consisted of fish prey. We documented a similar increase with fish size, including 8% for age two (180 to 259 mm) and 39% for age three and older brown trout (> 260 mm). In contrast, in many river systems, brown trout feed strictly on invertebrates (Kara and Alp, 2005; Montori et al., 2006). We hypothesize that high densities of sculpin and their low mobility (McCleave, 1964) contribute to such high rates of piscivory on the Logan River.

The actual percentage of sculpin we observed in diets varied widely among reaches, age groups, and individual fish in a reach. Most brown trout were either not piscivorous (~0%) or almost entirely piscivorous (~100%). Variation in the switch to piscivory between individual brown trout could result from spatial variation in sculpin versus invertebrate densities (Jensen et al., 2008), stochasticity in prey encounter histories (DeAngelis et al., 1991), and individual

variation in foraging ability and dominance (Graeb et al., 2005). Individual variation in foraging ability and dominance may result from differences in growth and gape limitation among individuals, an advantage which begins to manifest at an early age. For example, size at hatching and emergence, as well as the amount of invertebrates consumed, significantly influence early growth and the age at which piscivory occurs (Jonsson et al., 1999). Similar variation in piscivory has been observed for other species (Mittelbach and Persson, 1998), including largemouth bass (*Micropterus salmoides*) and walleye (Post, 2003; Graeb et al., 2005). Such individual variation in diets can contribute to within-population variability.

Our results suggest that brown trout predation does not control sculpin population abundance in the Logan River system. Our estimates of population densities are relative measures. Nonetheless, we observed higher densities of sculpin in reaches with the highest densities of brown trout, indicating that brown trout presence is not necessarily causing the low densities of sculpin. Similarly, co-occurrence of the two species has also been documented in other studies conducted in the Intermountain West (Bailey, 1952; Maret, 1997; Burbank, 2011). While we did observe consumption that exceeded estimated reach-scale sculpin abundance, we did not measure growth, survival, or recruitment rates. Quantification of these vital rates would be necessary to quantify the impact of exotic brown trout on sculpin population dynamics.

Even if brown trout do not significantly affect sculpin abundance, brown trout may have other effects on sculpin population dynamics. For instance, growth rates and fecundity of sculpin populations can increase in response to predation pressure by brown trout (Anderson, 1985); however, the mechanisms driving that response have not been fully explored. The potential for complex interactions between brown trout and sculpin in stream communities should be considered in efforts to understand the impacts of exotic brown trout on native sculpin. We note, however, that co-occurrence with brown trout may provide benefits to sculpin in some systems. For example, native sculpin have been shown to feed on brown trout eggs and fry (Berejikian,

1995; Palm et al., 2009) and to outcompete young brown trout within streams in brown trout's native range (Hesthagen and Heggenes, 2003). Even on the Logan River, isolated instances of mottled sculpin predation on age-0 brown trout have been documented during stream surveys. The outcome of interactions between sculpin and brown trout in river systems likely depends on the population structure and growth rates of both species, as well as abiotic habitat variables that characterize the physical template of the river.

The case of a novel predator: Ramifications for native fish communities?

Although these native mottled sculpin evolved with a salmonid predator, large brown trout on the Logan River exhibit rates of piscivory that are up to 50% higher than those of the large native cutthroat trout (McHugh et al., 2008). In addition, we demonstrated that brown trout consume large quantities of sculpin that exceeded rates of cannibalism and predation on other salmonids. Fluvial cutthroat historically present in the system likely consumed more sculpin than currently present, non-fluvial cutthroat trout. However, such predation would have likely been more seasonal in nature. In addition, other research has demonstrated that large, fluvial cutthroat trout consume significantly fewer fish than large brown trout of the same size (Sepulveda et al., 2009). These patterns suggest that brown trout represent a novel predator in this system. In a wide range of systems, exotic predators have greater impacts on native prey than native predators, because the prey lacks avoidance behaviors associated with the exotic predator (Salo et al., 2007). Factors contributing to lower piscivory by cutthroat trout remain unknown but could include lesser aggressiveness of cutthroat trout, greater efficiency of brown trout in capturing prey, or cutthroat trout selection of habitats with lower sculpin densities.

Further research should be conducted to study the impact of exotic brown trout on native fish communities, in general. Brown trout have been implicated in the decline of fish species worldwide (McIntosh et al., 1994; Macchi et al., 2007) and have dramatically altered native fish

communities (Garman and Nielsen, 1982; Flecker and Townsend, 1994) and even ecosystem processes (McIntosh and Townsend, 1996; Simon and Townsend, 2003). However, to date there has been considerably less focus on the impacts of brown trout predation relative to competitive interactions (Fausch, 1989; Taniguchi and Nakano, 2000; McHugh and Budy, 2006). In systems such as the Logan River, effects of brown trout predation on native fish populations may be difficult to evaluate because brown trout have been present for many years (i.e, since 1800's) and may have developed behaviors that reduce predation risk (Anderson, 1985). Therefore, evaluating effects of brown trout may require a combination of research approaches. Experimental manipulations designed to document behavioral interactions between brown trout and native fishes, community and population-level responses of naive and non-naive communities to brown trout consumption, and differences in the trophic structure of communities with and without brown trout would all contribute to our understanding of predatory impacts of exotic brown trout on native ecosystems.

CONCLUSIONS

In summary, our research illustrated high rates of predation on native mottled sculpin by exotic brown trout on the Logan River, Utah. In the presence of sculpin, large brown trout on the Logan River became highly piscivorous, in contrast with historical rates of piscivory by Bonneville cutthroat trout in the Logan River system (e.g., low to absent). This high piscivory by brown trout may contribute to their invasion success, including achieving high densities and growth rates, in portions of the watershed where brown trout and sculpin co-occur. Such high rates of piscivory may ultimately affect the population structure and viability of sculpin populations on the Logan River and beyond.

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CHAPTER 5

SUMMARY AND CONCLUSIONS

Exotic species are one of the greatest threats to biodiversity world-wide. However, in many systems, management objectives include both maintaining populations of introduced exotic species for recreational purposes while simultaneously conserving aspects of the native community. Additional research on factors influencing the establishment, spread, and potential negative impact of such introduced species could inform management and conservation efforts in systems where native and exotic species co-exist. In river systems, the success of introduced species is often dependent on the availability of suitable abiotic conditions, some of which vary predictably with broader scale landscape and watershed characteristics. Thus, by studying changes in ecological processes in relation to these patterns, we can better predict the invasion success and impact of introduced aquatic species within high-quality native communities.

For example, brown trout is one of the world's most successful invasive species that has been introduced to river systems world-wide for recreational fishing (Lowe et al., 2000; McIntosh et al., 2011). The invasion success of brown trout in river systems has been attributed to many factors, including the species' generalist habitat requirements and competitive ability (Flecker and Townsend, 1994; Heggenes, 2002), as well as the amount of brown trout introductions to a system (Westley and Fleming, 2011). In addition, extensive research has been performed to document brown trout life history, habitat requirements, and interactions with other species (Jonsson et al., 1999; Armstrong et al., 2003). Even so, further research on how the physical template of river systems influences brown trout abundance and survival could help in efforts to predict the potential spread of brown trout as a function of habitat alterations or climate change. Furthermore, in portions of rivers where brown trout have successfully invaded, a better

understanding of the negative impact of brown trout on native fish species and communities could be used in prioritizing conservation efforts.

These questions and uncertainties are relevant to the Logan River, where populations of both brown trout and native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) thrive. The Logan River exhibits a longitudinal decrease in brown trout density with increasing distance upstream, in contrast to increasing density exhibited by Bonneville cutthroat trout, a native species of conservation concern. Such patterns exist throughout much of the introduced range of brown trout (Bozek and Hubert, 1992; Weigel and Sorensen, 2001). Previous research on the Logan River suggests that abiotic factors limit the upper distribution of brown trout, allowing cutthroat to thrive in upstream portions (de la Hoz Franco and Budy, 2005; McHugh and Budy, 2005; Wood and Budy, 2009). However, this research has not conclusively determined the abiotic factors that most influence the distribution of brown trout (Budy et al., 2008). Further, while competitive interactions between brown trout and cutthroat on the Logan River have also been previously investigated, research has not yet addressed the potential for brown trout predation on native fishes. For my dissertation research, I investigated how characteristics of the river's physical template influence spawning gravel scour, gravel availability, and the longitudinal distribution of brown trout. In addition, I evaluated the potential for brown trout predation on a native fish—the mottled sculpin. Below, I summarize the general findings of this research and implications for brown trout management efforts.

The population dynamics of brown trout (*Salmo trutta*) fluctuate in response to flood magnitude, and eggs and fry of brown trout are susceptible to scour and displacement during flood events due to the mobilization of streambed gravels. Such scour can cause mortality of these early life-stages and could contribute to patterns of brown trout abundance in river systems. In chapter one, I evaluated how hydro-geomorphic factors describing the physical template of the Logan River influenced longitudinal trends in spawning gravel scour and potential for fry

displacement during typical spring flood events. I demonstrated that scour depths in spawning gravels did not significantly increase with distance upstream during either 2009 or 2010, and that scour depths were generally less than estimated depths of developing fry. A preference for areas of the channel with low entrainment potential contributed to shallow scour depths observed at spawning gravels across reaches, despite increases in reach-scale potential for entrainment. These results indicate that the potential for scour-related mortality of developing brown trout fry is low across all reaches during spring floods at magnitudes equal or less than bankfull. As a result, this mechanism is unlikely to contribute to lower densities of brown trout at upstream reaches. Nevertheless, recently-emerged or emerging fry in upstream reaches could still be susceptible to displacement, because they emerge closer to the time of the peak flood event compared to downstream reaches.

The distribution of brown trout in river networks may also depend on the availability of suitable spawning gravels, but few studies have compared the influence of gravel availability versus other abiotic factors in predicting brown trout distributions. In chapter two, I used a Bayesian hierarchical model approach to explore the role of multiple abiotic factors in predicting redd densities and the overall distribution of brown trout adults. I demonstrated that unit stream power can be used to predict areas of deposition, and potential spawning gravel accumulation, in river networks. In addition, I illustrated that remotely-derived unit stream power may be used in place of field measures to identify areas of spawning gravel accumulation, particularly in systems characterized by a wide range of stream gradients. Nevertheless, because the relationship between unit stream power and spawning gravel availability may differ by river system and fish species, further research should be conducted to verify the applicability of this approach.

Contrary to my prediction, unit stream power was not the top-performing predictor variable. The general increase in redd densities with distance upstream was best described by predictor variables describing the distribution of anchor ice, followed by variables describing

average temperature or distance upstream from Third Dam (a high density source area). Unit stream power was included in top models, but only in combination with these other measures. Thus, while gravel availability may have some influence on redd densities and overall invasion success, other propagule pressure or temperature-related factors are potentially more important. Given the strong correlation among these top predictors (anchor ice barrier, average temperature, distance upstream), they may all contribute to the lack of brown trout at high elevations. However, the model which included anchor ice as a barrier greatly outperformed the other models. Because much of brown trout movement occurs during spawning (Young et al., 1997), the presence of anchor ice during the spawning season could limit brown trout movement upstream, access to spawning gravels, and ultimately adult densities. Overall, my results demonstrate that abiotic habitat factors important to multiple life stages may control brown trout distributions on the Logan River.

While my first two chapters evaluated changes in the river's physical template in relation to patterns of brown trout abundance, my third chapter investigated the potential for exotic brown trout predation on a native fish—the mottled sculpin. I demonstrated that mottled sculpin abundance was significantly correlated with geomorphic variables (gradient (-), width (+), and median substrate (+)), while brown trout abundance was significantly correlated with temperature variables (annual minimum (+), average (+), and maximum temperature (+)). Sculpin abundance was not strongly correlated with brown trout densities, and reaches containing high densities of sculpin also exhibited some of the highest brown trout densities. In reaches where the two species co-occurred, brown trout consumed large quantities of sculpin which exceeded cannibalism rates and rates of predation on other species. Therefore, predation by brown trout could have other, currently unexplored, effects on sculpin population dynamics. Further, because mottled sculpin comprised a large portion of the brown trout energy budget in reaches where the two species co-occurred, this piscivory has potentially contributed to the high growth and

invasion success of brown trout in these reaches. These results suggest that brown trout is a novel predator in this system, with the potential to impact sculpin populations.

Conclusions and suggestions for future research

My results contribute to a better understanding of how brown trout distributions could respond to climate change and habitat alterations, and could be used to inform management efforts in this and similar systems. While mortality due to spawning gravel scour is an unlikely mechanism influencing the longitudinal distribution of brown trout on the Logan River, mortality due to displacement could still limit densities at high-elevation, upstream reaches (Wood and Budy 2009 and Chapter 1). Therefore, my results suggest that earlier flood events (as predicted to occur in this region with climate change) could actually result in lower densities of exotic brown trout in upstream reaches containing native cutthroat trout.

Further, even though temperature is often thought to be a strong driver of brown trout abundance, I demonstrated that factors limiting the longitudinal distribution of brown trout in the Logan may not be directly related to temperature (e.g., growth, reproduction). Instead, abiotic habitat factors which can co-vary with temperature, but may be unrelated or indirectly related (e.g., distance from high-density source areas and anchor ice as a barrier to movement), may ultimately limit distributions. In portions of river networks containing important native communities with low densities of brown trout, native fish conservation efforts could focus on identifying source areas (e.g., reservoirs and tributaries with high brown trout densities), and creating and maintaining barriers between these areas and the high-quality habitats. Because changes in the distribution and timing of anchor ice formation are difficult to predict, research efforts should focus on monitoring changes in anchor ice cover, and documenting the movement and population-level response of brown trout and native communities to these changes.

Finally, my research highlights strong predation pressure by brown trout on native mottled sculpin in the Logan River, higher than the extent and magnitude of predation pressure previously documented for native Bonneville cutthroat trout (McHugh et al., 2008). Additional research is needed to document potential negative impacts of exotic brown trout predation at the population and community levels. Such research could include conducting manipulative experiments to document behavioral responses of naive prey and communities to introductions, and to compare the population dynamics of native communities in stream systems with and without brown trout. Such research should be conducted in many stream types, due to the potential effects of varying abiotic factors on interactions between brown trout and prey communities. In many systems, maintenance of brown trout populations may be desirable due to relatively low impacts on native communities and/or the influence of more influential anthropogenic stressors. However, in protected and important native communities, negative effects of brown trout could be minimized through brown trout removal, increased fishing pressure, or other management activities.

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CURRICULUM VITAE

Christy Starr Meredith

csmeredith@fs.fed.us
https://sites.google.com/site/christysmeredith

United States Forest Service
PIBO Effectiveness Monitoring Program
860 North 1200 East
Logan, UT 84322-5210
(435) 755- 3597

Education

Fall 2006 – Present **Phd in Ecology, Utah State University Watershed Sciences Dept.**
Summer 2012
PhD Dissertation: "Factors influencing the distribution of brown trout (Salmo *trutta*) in a mountain watershed: implications for brown trout invasion success" with Dr. Phaedra Budy

2000-2002 **Master of Science in Water Science, Murray State University**
Awards: Sigma Xi Graduate Research Award Recipient
Master's Thesis: "Embryonic and larval response of three amphibian species to increasing nitrate concentrations" with Dr. Howard Whiteman

1995-1999 **Bachelor of Science in Environmental Science, Allegheny College**
Major: Environmental Science, Minor: Economics
Awards: Departmental Honors, Alden Scholar
Undergraduate Thesis: "How much is Enough? How Simple Livers are Showing that Less Can Be More"

Fall 1998 **Semester in Environmental Science**
Marine Biological Laboratory, Woods Hole, MA

Research Experience

2006 – present **Utah State University Watershed Sciences Department**
Graduate research assistant, Fish Ecology Lab- assist with fish mark-recapture surveys on the Logan River, manage temperature and stage height recorders, perform GIS analyses

My dissertation research focuses on geomorphic, hydrologic, and biological factors influencing the success of brown trout in the Logan River, Utah. The components of my dissertation include 1) investigating effects of the geomorphic template on the scour of brown trout spawning gravels along a longitudinal gradient 2) predicting the spatial distribution of brown trout spawning locations on the Logan River using stream habitat characteristics, 3) determining abiotic factors influencing the occurrence of brown trout and native mottled sculpin (*Cottus bairdi)*, as well as the bio-energetic contribution of mottled sculpin to the brown trout energy budget at reaches across the watershed.

2000-2002 **Hancock Biological Station on Kentucky Lake Reservoir**

Graduate research assistant- collected and analyzed reservoir and stream samples for inorganic and organic nutrients, chlorophyll a, and other parameters; performed macro-invertebrate and fish surveys for national assessment project; supervised undergraduates in the field and lab; and provided educational programs for visiting students

1996-1999 **Collegiate Research for Undergraduates Institutions (CRUI)**

Student research position, Allegheny College Environmental Science Department- conducted cation, nutrient, organic matter, and moisture analysis of soil samples; included a summer of soil science research at Harvard Forest in Petersham, MA

Professional Experience

February 2012-
June 2012 **United States Forest Service, PACFISH/INFISH Effectiveness Monitoring Program, Logan, Utah (GS11, term)**

Fish Biologist/Data Analyst-Provide statistical analysis and interpretation of fish habitat data; investigate how land management strategies influence health of aquatic habitat used by steelhead and bull trout within the Columbia River Basin

June 2007-
January 2009 **United States Forest Service, Logan Utah (GS5, Series 0404)**

Technician- Conducted field work related to geomorphic factors influencing fish distributions on the Logan River; performed Geographic Information Systems analyses (specifically regarding a model to predict fire potential during the field season)

2002-2006 **Western Pennsylvania Conservancy, Freshwater Conservation Program and Watershed Assistance Center**

Watershed Resources Specialist- served as project manager and lead scientist for various assessment projects, including acid mine drainage, watershed, and aquatic biodiversity assessments; helped watershed groups with grant writing, training, and outreach activities; developed and conducted watershed education programs

1999-2000 **Jesuit Volunteer Corps, Abused Women's Aid in Crisis Anchorage, AK**

Counseled and advocated for victims of domestic violence; responsibilities included initial screening of victims, advocating for victims at courthouse, conducting individual counseling sessions, and facilitating support groups

Teaching Experience

Graduate Teaching Assistant, Department of Watershed Sciences, Utah State University

♦ Introduction to Geographic Information Systems Laboratory (2007, 2008)
-wrote and taught exercises related to various aspects of GIS analysis
-conducted individual help sessions to assist students with weekly lab assignments and class projects

♦Limnology (2008)
-assisted primarily with grading of weekly assignments pertaining to the mathematics of limnology

♦Fish Diversity Laboratory (2009)
-developed and gave weekly lab lectures involving life history, identification, and anatomy of North American fishes

-conducted weekly lab sessions on fish identification and developed and graded tests

Visiting Instructor

♦ " Fish Diversity," Utah State University (Fall 2009) on "Feeding and Energetics"
♦ "Quantitative Field Methods," Allegheny College (2005) on "Using Science to Develop Management Objectives"
♦ "Non-major Ecology," Washington and Jefferson University (2005, 2006) on "Monitoring of Salamander populations in the Buffalo Creek Watershed"
♦ "Watershed Ecology,"California University of Pennsylvania (2004) on "Visual Assessment Protocols for Monitoring of Aquatic Health"

Scientific Presentations and Posters

♦ Meredith, Christy, P. Budy, and J. Schmidt. "The relative influence of temperature versus geomorphic factors on invasion potential of brown trout (*Salmo trutta*) in a mountain stream" presentation at the National American Fisheries Society Conference, Pittsburgh, PA (2010).

♦Meredith, Christy, P. Budy, and J. Schmidt. "The influence of geomorphic-hydrologic factors on invasion potential of brown trout (*Salmo trutta*) presentation at the Western Division of the American Fisheries Society Annual Meeting, Salt Lake City, UT (2009).

♦ Meredith, Christy and Phaedra Budy. "Understanding Limits to Brown Trout Invasion: Influences of Hydrologic and Geomorphic Factors" presentation at the Ecological Society of America Conference, Albuquerque, NM (2009)

♦ Meredith, Christy, Matt Baker, and Robert Gresswell. "Landscape, Network, and Pool Metrics Affecting Distribution and Abundance of *Oncorhynchus Clarkii clarkii* in 40 Watersheds in Western Oregon" poster presented to the North American Benthological Society Annual Meeting, Salt Lake City, UT (May 2008).

♦ Meredith, Christy. "Sublethal and lethal effects of nitrate on embryos and larvae of three amphibian species," presentation at the Society of Conservation Biology Conference (2003).

♦Meredith, Christy. "Diversity of an oak forest following additions of nitrogen-rich waste water," unpublished manuscript and presentation, presented at Woods Hole, MA as part of completion of Semester in Environmental Science research (1998)

♦Meredith, Christy and Richard Bowden. "Effects of past land use on soil moisture properties in an oak forest in Massachusetts," presentation at the Harvard Forest Student Research Symposium (1996) and Thiel College Student Research Symposium (1997)

Peer-reviewed Papers

♦ Meredith, Christy, and P. Budy, J. Schmidt, and M. Hooten. "Predicting the spatial distribution of brown trout (*Salmo trutta*) spawning densities: the role of gravel availability versus other habitat factors." In prep for *Canadian Journal of Fisheries and Aquatic Sciences*.

♦Meredith, Christy, G. Thiede, P. Budy, and J. Wood. "Predation on native mottled sculpin (*Cottus bairdi*) by exotic brown trout (*Salmo trutta*): the case of a novel predator?" In prep for *Ecology of Freshwater Fish*.

♦ Meredith, Christy, P. Budy, and J. Schmidt. "Potential scour of brown trout (*Salmo trutta*) spawning gravels along a longitudinal gradient of the Logan River, Utah." In prep for *River Research and Applications*.

♦ Meredith, Christy, and Howard Whiteman. 2008. "Effects of nitrate on embryos of three amphibian species," *Bulletin of Environmental Contamination and Toxicology 80: 529-533.*

Reports

♦ "Buffalo Creek Watershed Assessment and Protection Plan." Western Pennsylvania Conservancy (2006).

♦ "Blackleggs Creek Watershed Assessment and Acid Mine Drainage Restoration Plan." Western Pennsylvania Conservancy (2005)

♦ "Shenango Watershed Conservation Plan." Biological Assessment Chapter. Western Pennsylvania Conservancy (2004).

♦ "Three Sisters Watershed Conservation Plan." Biological Assessment Chapter. Western Pennsylvania Conservancy (2004).

Journal Peer Reviewer

- ♦ Journal of Herpetology
- ♦ Integrated Environmental Assessment and Management
- ♦ North American Journal of Fisheries Management
- ♦ Transactions of the American Fisheries Society
- ♦ Ecology of Freshwater Fish

Organization/Committee Involvement

- ♦ President, USU Student Subunit of Utah Chapter of the American Fisheries Society (2007-2009)
- ♦ Vice President, USU Student Subunit of Bonneville Chapter of the American Fisheries Society (2006-2007)

- Bridgerland Literacy Volunteer Tutor (2007-2009)
- Member, Utah State University Ecology Center Speaker Selection Committee (2006-2007)
- Board Member, Blackleggs Watershed Association and Trout Nursery (2005-2006)
- Big Sister, Big Brothers/Big Sisters (2004-2006)

Grants/Fellowships Awarded

- Utah State University graduate research extension grant ($5000, 2011)
- Kalamazoo Chapter of Trout Unlimited George L. Disborough Award ($1500, 2010)
- Utah State Ecology Center, Stipend and Project Award ($12000, 2007-2008)
- Special Project Award, Bonneville Chapter of the American Fisheries Society ($500, 2007)
- Utah State University, Vice-Presidential Fellowship ($15000, 2006-2007)
- Pennsylvania Coldwater Heritage Project Award, Laurel Run (2005, $5000)
- Altria Group, Shenango Algaewatch Monitoring Program Grant (2005, $20000)

Awards and Recognition

- Utah State University Ecology Center Conference Travel Award (2010)
- Utah State University Graduate Student Senate Conference Travel Award (2010)
- Utah Chapter of the American Fisheries Society, Award of Merit (2010)
- Terri Lynn Steel Memorial Award (2009)

Other Key Skills and Experience

- Experienced in methods to collect fisheries data and characterize fish populations, including electro-shocking, snorkeling, mark-recapture (MARK), 3-pass depletion, bio-energetic modeling (Bioenergetics 3.0) and use of the program R for calculation of population statistics

- Proficient in of a wide range statistical methods, with emphasis on multivariate (Classification and Regression Trees, Random Forests, Principal Components Analysis), and spatial statistics (areal analysis, geostatistics, point analysis)

- Proficient in use of ArcGis, Python, and Arc Macro Language (AML)

- Knowledge of a wide range of equipment used to measure physical characteristics of streams including total stations, auto-levels, bridge-carts (for development of stage-discharge relationships), and satellite gps units.

- Trained in use of limnological field equipment such as flow meters, d-nets and kick nets, light meters, schindler traps, secchi disks, eckman grabs, etc.

- Experienced in preparation of samples and standards for soil and water analyses, such as soil cations, chlorophyll a, total organic carbon and nitrogen, inorganic and organic nutrients, and proficient in operation of laboratory equipment such as LACHAT Quick-chem Autoanalyzers, carbon-nitrogen-hydrogen analyzers, and spectrophotometers

- Utah State University shortcourses attended: Bio-climactic Modelling (BIOMOD), Structural Equation Modelling, and Bayesian Statistical Techniques

References:

Phaedra Budy
Assistant Professor, Associate Coop Leader
USGS Cooperative Fish and Wildlife Research Unit
Department of Watershed Sciences
5210 Old Main Hill, Utah State University
Logan, UT 84322-5210
435-797-7564
Phaedra.Budy@usu.edu

Mevin Hooten
Assistant Unit Leader
Colorado Cooperative Fish and Wildlife Research Unit
Department of Fish, Wildlife, and Conservation Biology
Colorado State University
Fort Collins, CO 80523-1484
(970) 491-1415
Mevin.Hooten@colostate.edu

Brett Roper
National Aquatic Monitoring Program Leader
U. S. Forest Service, Forest Sciences Laboratory
860 North 1200 East
Logan, UT 84322-5210
(435) 755- 3566
broper@fs.fed.us